A regional examination of the mistletoe host species inventory

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Abstract: Downey (1998) collated an inventory of mistletoe host species based on herbaria records for every aerial mistletoe species (families Loranthaceae and Viscaceae) in Australia. In this paper the representative nature of those host lists is examined in an extensive field survey of mistletoes and their host species in south-eastern New South Wales (including Australian Capital Territory). Four new host species not in the 1998 inventory, and eight new mistletoe-host combinations (i.e. a previously recorded host but not for that particular mistletoe species) were collected. These new records were distributed throughout the survey area. Interestingly, these new host-mistletoe combinations were for mistletoe species that were well represented in the national inventory (i.e. with many herbarium collections and numerous host species). The initial inventory was incomplete, at least for south-eastern New South Wales, indicating the need for (i) more targeted surveys similar to this one, and/or (ii) regular updates of the host inventory based on voucher specimens. A possible reasons why information on host-mistletoe combinations is incomplete may be that such combinations may be dynamic (i.e. mistletoe species may be expanding their suite of potential hosts, either fortuitously or as result of evolutionary pressures).

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Introduction

Hemi-parasitic mistletoes are often considered to be host-specific i.e. certain mistletoe species occur on a select range of host species (Kuijt 1969, Barlow & Wiens 1977, Barlow 1981, Atsatt 1983, Reid et al. 1995, Norton & de Lange 1999). The term low host specificity has been used to describe mistletoe species which have many unrelated host species, and the term high host specificity when mistletoe species are restricted to one or a few related host species (Barlow & Wiens 1977, Atsatt 1983). Host specificity implies a one-way interaction, that of the mistletoe. The role the host plays in this parasitic interaction is rarely considered to be important, implying the host has no or little influence on the parasitic process. However, the host can play a role in determining its parasitic constituents, through host resistance to haustorial penetration (Kuijt 1969, Hariri et al. 1987, Yan 1993) and chemical incompatibility (Kuijt 1969). There is a considerable number of plant species which are not host species, other than the obvious herbaceous and annual species, which are incapable of sustaining mistletoes due to their growth forms and size (i.e. Downey (1998) only recorded 873 host species of an Australian vascular flora of 20 000 species). Therefore the relationship between a host and a mistletoe can be a two way interaction, and the combination between hosts and mistletoes can be described as either a host-mistletoe combination (i.e. the host species for each mistletoe species, for example, *Amyema miquelii* has 125 host species, Downey 1998) or a mistletoe-host combination (i.e. the mistletoe species for each host species, for example, 17 mistletoes parasitise *Acacia aneura,* Downey 1996).

Theoretically, before a mistletoe species can be described as host-specific, a comprehensive list of its recorded host species must be collated from throughout its range. However, such lists, for any of the 88 aerial Australian mistletoe species, were unavailable prior to the host inventory of Downey (1998). The initial national host inventory was collated from records of the major Australian herbaria but was incomplete: five mistletoe species had no recorded host species, and some hosts were only documented to genus level. The incompleteness of the host inventory may be attributed to inadequate host collection.

Collection of hosts many be influenced by local conditions. For example, the type and number of plant species, and structure in a particular community can influence the number of host species available for colonisation (Hoffmann et al. 1986), and the dynamics of a community can influence the mistletoe species composition (Overton 1994, Dean et al. 1994, Downey et al. 1997). Furthermore, the number of potential host species present in any one location may not reflect the number of mistletoes species present. As an extreme example, Tasmania has numerous species that are recorded as mistletoe hosts on mainland Australia, but the island State has no mistletoe species present (Downey 1996). To evaluate the completeness of mistletoe host species lists, some scale (i.e. local or regional) of ground-truthing needs to be undertaken. This study examines host-mistletoe combinations in south-eastern New South Wales and compares them with the national host inventory compiled by Downey (1998).

Table 1. The mistletoe species present in the study area and information on their host species nationally (after Downey 1998).

Mistletoe species	Distribution in Australia	Distribution within study area	Number of specimens nationally	Number of host species nationally	Number of host families nationally
Loranthaceae					
Amyema cambagei (Blakely) Danser	Eastern Australia	widespread	258	10	5
Amyema congener (Sieber ex Schultes & J.H. Schultes) Tieghem	E & N Australia	coastal	340	90	31
Amyema miquelii (Lehm. ex Miq.) Tieghem	Australia wide	widespread	919	125	10
Amyema pendula (Sieber ex Sprengel) Tieghem	Eastern Australia	widespread	399	75	6
Dendrophthoe vitellina (F. Muell.) Tieghem	Eastern Australia	coastal	346	76	29
Muellerina bidwillii (Benth.) Barlow	Eastern Australia	non-coastal	60	6	2
Muellerina eucalyptoides (DC.) Barlow	Eastern Australia	widespread	194	43	22
Viscaceae					
Notothixos cornifolius Oliver	Eastern Australia	non-coastal	105	8	4
Notothixos subaureus Oliver	Eastern Australia	coastal	237	35	10

Table 2. Number and percentage of new hosts for three mistletoe species recorded from south eastern NSW

Mistletoe species	Number of new host species	Number of host species (Downey 1998)	Total number of host species	Percentage increase from SE NSW
Amyema miquelii	1	125	126	1
Amyema pendula	8	75	83	10
Muellerina eucalyptoides	3	43	46	7

Methods

A network of transects was established in south-eastern New South Wales (including the Australian Capital Territory) based upon the major roads between Wee Jasper and Batemans Bay, via Canberra. The straight-line distance between Canberra and Batemans Bay is approximately 100 km. A transect extending both north and south of Batemans Bay, was added to include coastal vegetation. The study area included sub-alpine, temperate and coastal vegetation communities.

Nine mistletoe species from two families are known from this area (Table 1), six from the Australian Capital Territory and surrounding region (Burbidge & Gray 1970) and another three between the Great Dividing Range and Batemans Bay (Quirico 1992a, b). Host species for each of these mistletoe species are in the national inventory (Downey 1998).

Each of the main and secondary roads within the study area was traversed, forming separate 'transects'. Smaller confined areas were also sampled in and around Canberra (e.g. Cooleman Ridge and Mulligans Flat Nature Reserve). Each time a mistletoe plant was observed, the host-mistletoe combination was determined. If the combination was unknown, or if the host species could not be identified in the field, a herbarium specimen was collected for both the mistletoe and the host species. Each individual collection was numbered with an 'a' for the mistletoe species and a 'b' for the host species after the collection number (e.g. POD 106a & POD 106b). The location of each host-mistletoe combination was mapped using GIS software. All specimens are now located in the Australia National Herbarium (CANB). Some observed occurrences could not be collected because the mistletoe species and/or the host species were too high to collect suitable material for identification. Combinations were checked against the national host inventory (Downey 1998) to determine if the mistletoe-host combination had been previously recorded in Australia.

Mistletoe taxonomy followed Barlow (1984a, b) and host taxonomy followed Wilson and Johnson (1989), Harden (1991) and Tame (1992). M.I.H. Brooker (CANB) identified all Eucalypt hosts, including species assigned to *Eucalyptus* and *Corymbia*.

Results

All nine mistletoe species known to occur in the study area were collected (Table 1) as well as 31 different host species, forming 38 different host-mistletoe combinations (Appendix 1). Twenty-six of these host-mistletoe collections were previously recorded in the national host inventory (Downey 1998).

Three mistletoe species had new host species (Table 2). The number of previously known host species for a mistletoe species in 1998 was not a predictor of the number of new host species that were observed for the same mistletoe species in the present study (Table 1, 2). New host species were only observed for mistletoe species that had more than 40 documented host species and more than 190 collections nationally (Table 1, 2). For example, a new host was collected for *Amyema miquelii*, the Australian mistletoe species with the greatest number of known host species

Table 3. New host-mistletoe combinations collected in south-eastern NSW.

Mistletoe species	Host family	Host species	Host status[1]	Native host species outside of their natural range	Previous number of host combinations[2]
Amyema miquelii	Myrtaceae	*Eucalyptus crenulata*	New	yes	0
Amyema pendula	Mimosaceae	*Acacia floribunda*		yes	2
	Fabaceae	*Chamaecytisus palmensis**		yes	7
	Myrtaceae	*Eucalyptus elata*	New	no	0
	Myrtaceae	*Eucalyptus globoidea*		no	1
	Myrtaceae	*Eucalyptus nicholii*	New	yes	0
	Myrtaceae	*Eucalyptus pauciflora*		no	1
	Myrtaceae	*Eucalyptus rubida*		no	1
	Fagaceae	*Quercus palustris**	New	yes	0
Muellerina eucalyptoides	Myrtaceae	*Eucalyptus dalrympleana*		no	2
	Myrtaceae	*Eucalyptus globoidea*		no	1
	Myrtaceae	*Eucalyptus radiata*		no	1

[1] As recorded by Downey (1998)
[2] The number of combinations each host species is known from i.e. in Downey (1998)
* denotes exotic or introduced species to Australia

Table 4. Host-mistletoe combinations collected from the study area with five or fewer records nationally (Downey unpub. data), and the total number of records for each host species.

Mistletoe species	Host species	No. of times the combination had been previously recorded	No. of time the host has been previously recorded in a combination
Amyema congener	*Acacia mearnsii*	2	59
Amyema miquelii	*Eucalyptus bicostata*	2	2
	Eucalyptus polyanthemos	2	23
Amyema pendula	*Eucalyptus cinerea*	2	3
	Eucalyptus mannifera	3	6
	Eucalyptus ovata	5	6
	Eucalyptus radiata	5	5
Muellerina eucalyptoides	*Acacia floribunda*	1	2
	Eucalyptus cypellocarpa	1	1
	Eucalyptus pauciflora	2	2
	Eucalyptus sideroxylon	4	17

(Table 2). *Amyema pendula* had the highest number of new host species and the greatest percentage change in the total number of known host species from the national inventory (Table 2).

A total of 12 new host-mistletoe combinations were collected (Table 3). Eight combinations comprised a host species that was already known as a mistletoe host (Downey 1998), but not for the mistletoe species collected here. One of these new combination (*Amyema pendula* on *Eucalyptus pauciflora*) was collected from two separate locations; another (*Amyema pendula* on *Quercus palustris**) from three. Seven of the eight combinations contained host species that were previously only known as host species for either one or two other mistletoe species (Table 3). The other four new combinations included a host species which was not previously known as a host species (i.e. not recorded by Downey 1998) *viz. Eucalyptus crenulata, Eucalyptus elata, Eucalyptus nicholii,* and the exotic *Quercus palustris** (Table 3). Locations of new combinations or new host species were dispersed throughout the study area (Fig. 1).

A further 11 combinations were poorly-documented i.e. known from less than six collections nationally (Table 4). Two of these combinations had only been collected once before.

Five of the new combinations had host species which were considered to be either non-indigenous (three hosts), in that they were Australian natives outside of their natural range, or introduced or exotic to Australia (two hosts: Table 3); one of these was a new host (*Amyema pendula* on the exotic *Quercus palustris**).

There were no additional host families observed, however, one mistletoe species, *Amyema pendula*, increased the number of host families it parasitised by two (Fagaceae and Fabaceae). *Eucalyptus* and *Acacia* species comprised the majority of host species.

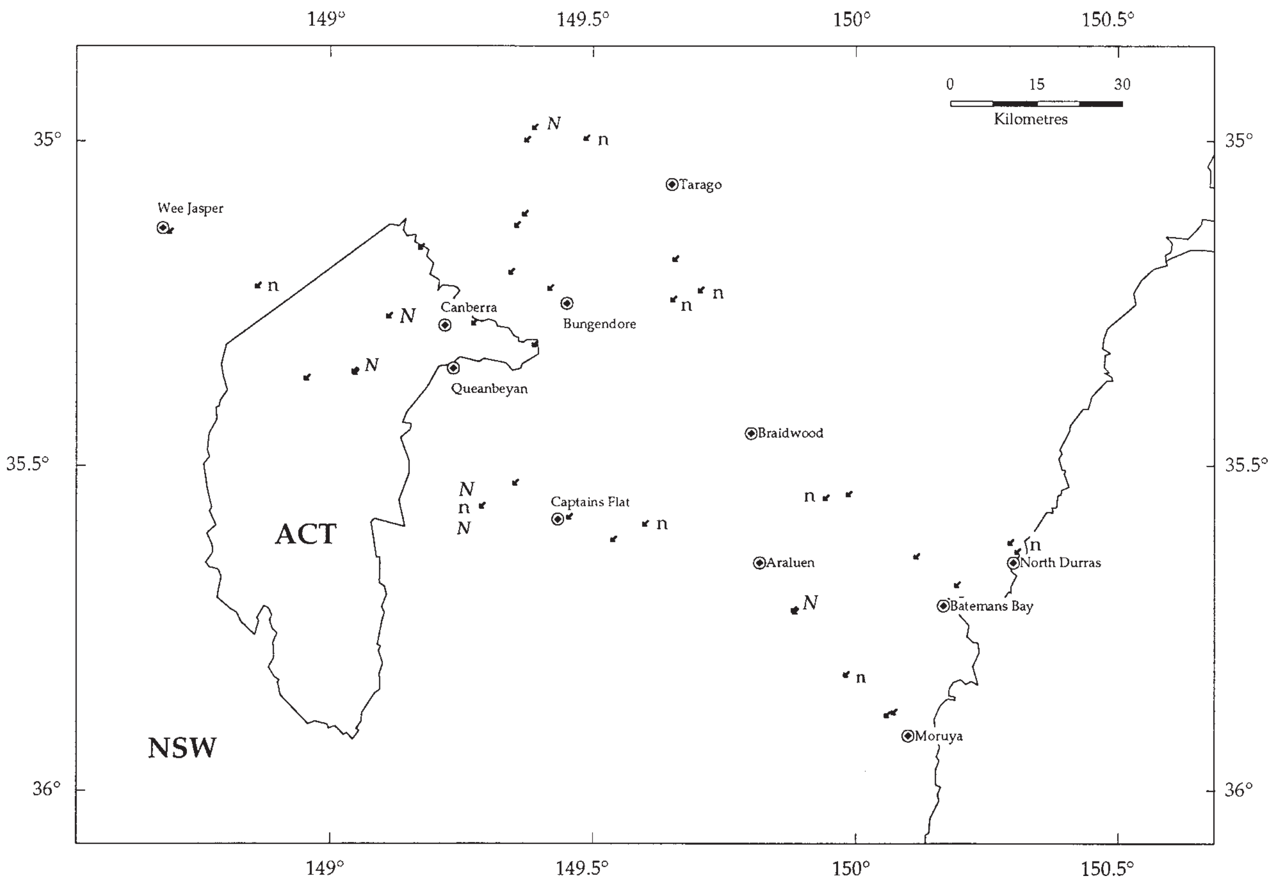

Fig. 1. The location of mistletoe and host collections (➹) made within the study area and the location of new host species (*N*) and host-mistletoe combinations (n).

Discussion

The present study showed that host-mistletoe combinations in southern New South Wales (including Australian Capital Territory) have not been thoroughly examined and suggests that the national host inventory (Downey 1998) is incomplete. The are several reasons why the host inventory may be incomplete: (i) mistletoe hosts are not always collected or identified correctly, which may bias information on host dynamics, (ii) dedicated investigation of host species have not occurred, (iii) in the absence of a host inventory new hosts maybe overlooked, or (iv) host-mistletoe combinations are dynamic in a number of ways.

(i) Collection of host species

Compilations of mistletoe host species from herbaria records may not encapsulate the complete set of host species, as illustrated by five mistletoe species that had no host records in the 1998 inventory (see Downey 1998). One of the problems with this host inventory is that it was derived from mistletoe collections, not host collections, and is incomplete, as hosts are not always documented. In addition, collectors do not typically collect or note the other host species that are present in the area, or collect the same mistletoe species close by on a separate host species (Barlow pers. comm.).

Host species are not collected for a number of reasons: (i) insufficient material to make an identification at the time of collection, (ii) collecting techniques employed, (iii) collector's knowledge of the host species, or (iv) height of the host. For example, the specimen of *Muellerina eucalyptoides* collected here from *Eucalyptus cypellocarpa* was approximately seven metres from the ground and the host tree was approximately 45 metres tall, with few branches below 20 metres; making a the collection of a herbarium specimen difficult. Similarly, no mistletoe collections have been made from *Eucalyptus regnans*, despite several reports of mistletoes growing on it (Patton 1917, Coleman 1949, A.M. Gill pers. comm.). Highlighting the difficulty of collecting from very tall trees, there are only 16 collections of *E. regnans* in the Australian National Herbarium (CANB).

(ii) Targeted mistletoe host surveys

Targeted mistletoe host surveys are rare, especially over a large area, like southern New South Wales. The only other published targeted survey was undertaken by Moss (1998) from south-east Queensland. Comparisons of Moss' (1998) host lists with the national host inventory revealed 50 new mistletoe-host combinations, from 90 combinations observed for 16 mistletoe species. Of these new combinations 23 contained new host species (i.e. not recorded in the national inventory). Apart from Moss (1998), host lists tend to be the result of generic surveys over a confined area. While such lists can add valuable information on host species, they may not reflect geographic variation in host species or the mistletoe species.

Downey (1996) found that the greater the number of mistletoe collections, the greater the number of host species; therefore targeted surveys could reveal new hosts, especially in poorly collected areas. The present targeted survey in part supports this finding in that new host species were only recorded for mistletoe species with many recorded collections and hosts. The widespread nature of these mistletoe species, with high collections and host numbers, may influence their ability to have many host species, as their distribution overlaps the distributions of many hosts (Downey 1996), and they are more likely to be collected. Targeted surveys which involve mistletoes that are poorly collected (or known) are likely to reveal new host-mistletoe combinations. For example, a localised survey of *Muellerina myrtifolia* from southern Queensland revealed three new mistletoe-host combinations and two new host species from six collections. The national inventory contained four host-mistletoe combinations (to species level and one to genus) from 24 collections of *Muellerina myrtifolia* (Downey unpub. data, Downey & Halasz in prep.).

On a local scale, there is a limited number of potential host species available for colonization at any one site. Nearby sites may contain different host species or different densities of host plants which may affect the suite of mistletoe species present at that location (Overton 1994). It is important to consider populations of mistletoe populations or mistletoe meta-populations when investigating their host species. The suggestion that host specificity at species rank occurs mainly on a local scale, has been put forward by Norton et al. (1995). This phenomenon may be based on the number of potential hosts available at a particular location, or it may be that a mistletoe species may only parasitise a portion of its total host set at a given location (Overton 1994). Either case may mislead observers into thinking that host specificity occurs over the entire distribution of the mistletoe, or on a national scale.

All nine mistletoe species collected within the study area had patchy or disjunct distributions on a local scale, supporting observations by others (e.g. May 1941, Norton et al. 1995). The spatial distribution of the new combinations (see Fig. 1) was dispersed throughout the study area.

Trees in roadside corridors in Western Australia contained very low densities of mistletoes compared with larger woodland fragments (Norton et al. 1995); elsewhere roadsides increase mistletoe density (Norton & Stafford Smith 1999). Roadside surveys like the current study could influence the number of hosts observed. Distribution data from 9000 Australian mistletoe specimens revealed a road map of Australia (Downey 1996), suggesting that the majority of herbarium collections are made along roads. Targeted host surveys need to account for variations in the landscape and not just sample roadsides.

(iii) Absence of a host inventory

In the absence of a host inventory some host species may be overlooked, as there is no way to determine if a host species is a new record. Some host species may be observed and noted on a regional basis (e.g. Moss 1998) but not collated anywhere. Such regional records were not included when the national host inventory was compiled but have been included in the revised inventory (Downey & Halasz in prep.). Herbarium vouchering of such observations may not occur or take a long time to occur, for example, Blakely (1922) noted *Amyema pendula* growing on *Chamaecytisus palmensis**, but it was not until the current study, some eighty years later, that this mistletoe-host combination was collected. The absence of a host inventory prevents analysis of the nature of mistletoe-host combinations. For example, *Quercus palustris** was not recorded in the host inventory, but was noted as a host for *Muellerina eucalyptoides* (Seebeck 1997) and *Amyema pendula* (here). The presence of a host inventory stimulates collection of hosts, and discussion and better understanding of host species.

(iv) The dynamics of host-mistletoe combinations

Host-mistletoe combinations may be dynamic. Evidence presented here suggests that mistletoe species have the ability to expand their suite of host species. Such expansions may occur either fortuitously through the introduction of exotic and/or native host species that are not indigenous to that area or as result of evolutionary pressures (Norton & Carpenter 1998, Norton & de Lange 1999) which might arise in response to environmental pressures like habitat modification (Norton & Stafford Smith 1999) and climate change (e.g. based on *Viscum album* in Europe, Jeffree & Jeffree 1996). The exact way in which host expansion occurs is not clear, but may result from these processes independently or from other factors like avian dispersers (Liddy 1983, Buen & Ornelas 1999, Lavorel et al. 1999), temporal component of relative host abundance (Norton & de Lange 1999), or any combination of these. Irrespective of these factors host expansion can be limited by the plants that mistletoes are dispersed to, as some plants can prevent mistletoe parasitism. For example, some host species have their own mechanisms for resistance to haustorial penetration and development. These mechanism include: bark resistance (Hoffmann et al. 1986, Hariri et al. 1987, Yan 1993); bark thickness (Littlejohns 1950); bark texture (Morgan 1914); branch diameter (Reid 1991); branch age (Liddy 1983); xylem resistance (Hoffmann et al. 1986, Yan 1993) and; previous infestation of the host (Hoffmann et al. 1986). Thus, host resistance may explain why some plants are free from infection (Hoffmann et al. 1986) and explain limitations to host expansion.

The floristic dynamics of the mistletoe-host combinations observed were not explored here, in part due to the small sample size. Examination of the major host genera (*Eucalyptus* and *Acacia*) and their mistletoe species at a national level has been inconclusive i.e. at the sub-generic level of *Eucalyptus* (Downey 1996), and at the time of writing, analysis of the updated host inventory (Downey and Halasz in prep.) is not available. New hosts identified since the host inventory (Downey 1998) show a wide floristic diversity (Downey unpublished data, Downey and Halasz in prep.), and examination of mistletoe distribution patterns show that mistletoe diversity is lowest where host diversity is low i.e. in arid Australia (see Downey & Gill in prep.). An analysis of the phytogeography of host-mistletoe combinations could not be undertaken due to the limited distribution data for many host species (see Downey & Gill in prep.).

The introduction of exotic species and expansion of native species to new ranges can lead to potential new (or ‘novel’) host species. Many exotic species have been recorded as mistletoe hosts (Johncock 1903, Blakely 1922, Hart 1961, Marshall 1981, Seebeck 1997, de Lange et al. 1997, Downey 1998, Downey & Halasz in prep.). The current study recorded several native host species outside of their natural range, highlighting the dynamic mistletoe-host interactions associated with ‘novel’ host species. The number of new combinations observed, increased where there was an increase in the number of native plant species outside of their natural range (e.g. private acreage near reserves in Canberra), suggesting that garden plants provide a substantial source of new hosts. The colonization of new hosts or host-switching may ultimately lead to mistletoe speciation (Norton & Carpenter 1998).

The number of introduced species globally has increased dramatically over the past 200 years (di Castri 1989, Reichard & Hamilton 1997) and the number of exotic hosts will increase in the future (Humphries et al. 1991). The number of mistletoe species which parasitise introduced species is likely to increase as these introduced species increase their distribution. For example, Seebeck (1997) noted *Muellerina eucalyptoides* growing on *Quercus palustris**, which was collected subsequently in this study as a host of *Amyema pendula*. Regular updates of the host inventory will allow the capture of these dynamic interactions. Similarly, there are several exotic species in Australia which are not known to be mistletoe hosts, but are known to host mistletoes elsewhere in their exotic range (e.g. *Cytisus scoparius* in New Zealand: de Lange et al. 1997, Downey & Halasz in prep.). The role introduced hosts play in mistletoe colonization needs further study. As mistletoe abundance varies between hosts (see Norton & Carpenter 1998, Buen & Ornelas 1999) the density of mistletoes on ‘novel’ and ‘normal’ hosts should be included in any such studies.

The ability of mistletoe species to parasitise species that they have never previously encountered makes the prediction of possible host species difficult, questions host-specificity and poses interesting management dilemmas. For example, the ability of endangered New Zealand mistletoes to grow on exotic species (de Lange et al. 1997, Downey & Halasz in prep.) may help their management (Reid 1998).

Conclusion

The national host inventory is incomplete at least in south-eastern New South Wales. There are several possible reasons for this incompleteness. Host-mistletoe combinations are dynamic and new host combinations with known mistletoe hosts are continuing to be documented. The reasons for the dynamic nature of host-mistletoe combinations include the presence of ‘novel’ (i.e. exotic or ‘non’-indigenous) host species. Targeted surveys like this one are extremely important to our understanding of host-mistletoe relationships.

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Appendix 1. Host-mistletoe combinations collected in the study

Mistletoe family	Mistletoe species	Host family	Host species
Loranthaceae	*Amyema cambagei*	Casuarinaceae	*Casuarina cunninghamiana*
	Amyema congener	Mimosaceae	*Acacia mearnsii*
	Amyema miquelii	Myrtaceae	*Eucalyptus bicostata*
		Myrtaceae	*Eucalyptus blakelyi*
		Myrtaceae	*Eucalyptus crenulata*
		Myrtaceae	*Eucalyptus polyanthemos*
		Myrtaceae	*Eucalyptus sideroxylon*
	Amyema pendula	Mimosaceae	*Acacia dealbata*
		Mimosaceae	*Acacia floribunda*
		Mimosaceae	*Acacia mearnsii*
		Mimosaceae	*Acacia melanoxylon*
		Fabaceae	*Chamaecytisus palmensis**
		Myrtaceae	*Eucalyptus bridgesiana*
		Myrtaceae	*Eucalyptus cinerea*
		Myrtaceae	*Eucalyptus elata*
		Myrtaceae	*Eucalyptus globoidea*
		Myrtaceae	*Eucalyptus macrorrhyncha*
		Myrtaceae	*Eucalyptus mannifera*
		Myrtaceae	*Eucalyptus nicholii*
		Myrtaceae	*Eucalyptus ovata*
		Myrtaceae	*Eucalyptus pauciflora*
		Myrtaceae	*Eucalyptus radiata*
		Myrtaceae	*Eucalyptus rubida*
		Myrtaceae	*Eucalyptus viminalis*
		Fagaceae	*Quercus palustris**
	Dendrophthoe vitellina	Myrtaceae	*Eucalyptus maculata*
	Muellerina bidwillii	Cupressaceae	*Callitris endlicheri*
	Muellerina eucalyptoides	Mimosaceae	*Acacia floribunda*
		Myrtaceae	*Angophora costata*
		Myrtaceae	*Eucalyptus blakelyi*
		Myrtaceae	*Eucalyptus cypellocarpa*
		Myrtaceae	*Eucalyptus dalrympleana*
		Myrtaceae	*Eucalyptus globoidea*
		Myrtaceae	*Eucalyptus pauciflora*
		Myrtaceae	*Eucalyptus radiata*
		Myrtaceae	*Eucalyptus sideroxylon*
Viscaceae	*Notothixos cornifolius*	Sterculiaceae	*Brachychiton populneus*
	Notothixos subaureus	Loranthaceae	*Muellerina eucalyptoides*

* denotes exotic or introduced species to Australia