
Lessons in Ecosystem Management from Management of Threatened and Pest Loranthaceous Mistletoes in New Zealand and Australia

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Abstract: *Loranthaceous mistletoes are interesting because of their complex dependence on suitable host trees and avian dispersers and because of their patchy distribution at the landscape level. Although their over- and under-abundance in Australia and New Zealand have been widely documented, little attention has been given to the need for an ecosystem approach to their management. Although the current status of mistletoes is very different in Australia and New Zealand, some of the causal factors and the long-term effects of changes in mistletoe abundance are similar in the two countries. We suggest that mistletoe abundance in pre-European landscapes was dependent on a series of evolutionary and environmental filters relating to host specificity, pollination, dispersal, infection, environmental habitat quality, predation, and disturbance. European settlement modified these filters in a number of ways, resulting in either increases or decreases in mistletoe abundance. The three broad groups of changes that have occurred with European settlement involve fragmentation, predation, and altered disturbance regimes. Although managers have usually addressed mistletoe over- or under-abundance with short-term solutions (e.g., pruning infected trees), we suggest that management must address the underlying causes of the problems involving mistletoes. This requires an ecosystem approach to management that addresses both the direct and indirect causes of the current status of mistletoes.*

Lecciones de Manejo de Ecosistemas Manejo de Muérdagos Lorantáceos Amenazados y Plagas en Nueva Zelanda y Australia

Resumen: *Los muérdagos lorantáceos son interesantes por su compleja dependencia de árboles hospederos adecuados y de aves dispersoras y por su distribución en parches a nivel de paisaje. A pesar de que su sobre- y baja- abundancia en Australia y Nueva Zelanda han sido ampliamente documentados, se ha prestado poca atención a la necesidad de un enfoque de ecosistema a su manejo. Aunque el estatus actual de los muérdagos es muy diferente en Australia y Nueva Zelanda, algunos de los factores causales y de los efectos a largo plazo de cambios en la abundancia de muérdagos son similares en ambos países. Sugerimos que la abundancia de muérdagos en los paisajes pre-europeos dependía de un serie de filtros evolutivos y ambientales relacionados con la especificidad del huésped, la polinización, infección, calidad del hábitat, depredación y perturbación. La colonización por europeos modificó estos filtros en numerosas formas, resultando en incrementos o decrementos en la abundancia de muérdagos. Los tres amplios grupos de cambios que han ocurrido con la colonización europea comprenden fragmentación, depredación y alteración de regímenes de perturbación. Aunque los manejadores generalmente abordan la sobre- o bajo-abundancia de muérdagos con soluciones a corto plazo (e.g. poda de árboles infectados), sugerimos que el manejo debe atender las causas que subyacen los problemas que involucran muérdagos. Esto requiere de manejo con enfoque de ecosistema que aborde tanto las causas directas como indirectas del estatus actual de los muérdagos.*

Introduction

Plants in the family Loranthaceae form the largest group of parasitic angiosperms, with at least 850 species in 65 genera (Thorne 1992). Together with the Viscaceae, Eremolepidaceae, Myzodendraceae, *Phacellaria*, and the 'Henslowia' complex in the Santalaceae, they form a polyphyletic group of shrubby aerial stem parasites commonly called mistletoes (Kuijt 1990; Reid 1991). Some Loranthaceae and Viscaceae species are serious pests in natural forests, plantations, orchards, and ornamental plantings throughout the world (Hawksworth 1983), where they significantly reduce productive outputs. A substantial literature has developed concerning the reasons for their pest status and management approaches to mitigate impacts (Hawksworth 1983; Hawksworth & Shaw 1984). There are also situations where mistletoe over-abundance does not threaten productive outputs but has serious implications for ecosystem condition (e.g., in parts of Australia; Reid 1995). In contrast, substantial declines in mistletoe abundance in some areas (e.g., New Zealand; Ogle & Wilson 1985; Norton 1991; de Lange & Norton 1997) also threaten ecosystem condition. Little attention has been paid to the importance of mistletoe over- and under-abundance for conservation and the management options for dealing with these situations.

Loranthaceous mistletoes are predominantly arboreal xylem parasites (Calder 1983), dependent on their host for water, nutrients, and to some extent carbon (Ehleringer et al. 1985; Marshall & Ehleringer 1990). This, together with their inter-dependence with birds for pollination and dispersal (Kuijt 1969; Reid et al. 1995) and their spatially heterogeneous landscape distribution (Norton et al. 1995), suggests that approaches to their management have to be landscape or ecosystem rather than single-species based. In particular, management actions that address short-term symptoms rather than underlying causes are unlikely to result in long-term improvements in mistletoe status or ecosystem condition.

The over- and under-abundance of loranthaceous mistletoes in Australia and New Zealand, respectively, is of particular interest because, although the current status of mistletoes is very different, some of the causal factors and the long-term effects of changes in mistletoe abundance are similar in the two countries. Furthermore, short-term solutions have failed to address the cause of the problem in both countries, which requires integrated ecosystem management. Therefore, management strategies for dealing with mistletoe abundance are likely to be similar in scope, although the specific actions will be different. Specifically, we address the following questions: (1) Under what situations are loranthaceous mistletoes over-abundant in Australia and under-abundant in New Zealand? (2) What are the natural regulators of mistletoe abundance that need to be considered in developing management strategies? (3)

What are the factors that have led to the current status of mistletoes in Australia and New Zealand? (4) What management approaches will address the causes of the problem in the two countries, rather than the symptoms? Because of the ecological similarities between loranthaceous and viscaceous mistletoes, we have drawn on the extensive Northern Hemisphere literature on viscaceous mistletoes where there is an absence of comparable information on loranthaceous mistletoes.

Current Status

Seventy-two species of loranthaceous mistletoe are recognized in Australia (Barlow 1984, 1992) and seven species in New Zealand (Barlow 1966; de Lange et al. 1997). Four of the six New Zealand genera are endemic, one extends to Norfolk Island (*Ileostylus*) and one is shared with Australia (*Muellerina*). Five of the 12 Australian genera extend into southeast Asia and the western Pacific, and the remaining genera are endemic.

Six of the seven New Zealand loranthaceous species are threatened with extinction or presumed extinct, and the seventh species is ranked as "local," a non-IUCN category (Cameron et al. 1995). Two are "presumed extinct" (*Trilepidea adamsii*, *Muellerina celastroides*), three are ranked as "vulnerable" (*Alepis flavida*, *Peraxilla colensoi*, *P. tetrapetala*) and one "rare" (*Tupeia antarctica*). In contrast only 5 of the 72 Australian species are ranked as threatened (Briggs & Leigh 1988; Leigh & Briggs 1992), but threats to these species are possible, reflecting their limited natural distribution, rather than actual. For example, *Dactylophora novae-guineae*, is "rare" in Australia, but is also present in New Guinea where it is more abundant.

In contrast to the rarity of New Zealand mistletoes, some mistletoe species have undergone marked local increases in abundance throughout the agricultural districts of southern and eastern Australia since 1900, especially *Amyema miquelii* and *A. pendulum* (Reid 1995). Although there is evidence of abundant mistletoe infestations in temperate and arid Australia in pre-European times, the increases in abundance since 1900 have resulted in tree debility and death and have caused considerable concern in rural communities. For example, mistletoes were declared noxious plants in Victoria in 1904 (Coleman 1949) and extensive control was undertaken in some districts. Whereas some mistletoe species (e.g., *Ileostylus micranthus* and *Tupeia antarctica*) are locally abundant in parts of New Zealand, especially in modified ecosystems, this appears to be localized rather than widespread as is the case in parts of Australia. Furthermore there is no evidence to suggest that the present abundance of some species in modified New Zealand ecosystems is substantially different from that which occurs in predominantly natural ecosystems (D. Norton unpubl. data).

Regulators of Mistletoe Abundance in Pre-European Landscapes

A number of aspects of mistletoe biology are crucial to understanding the reasons for their present status and associated management concerns. In pre-European landscapes a series of evolutionary and environmental factors or filters regulated the abundance of mistletoes. European settlement modified the influences on mistletoe abundance in both Australia and New Zealand in a number of ways, resulting in either increases or decreases. We review the filters or regulators that were most important in pre-European landscapes.

At the broadest spatial and temporal scales, major climatic gradients (Barlow 1981) and evolutionary history (Barlow 1983) determine the occurrence of individual mistletoe species (for example the occurrence of loranthaceous mistletoes on the remnants of Gondwana). At medium to fine spatial and temporal scales, five broad groups of factors are important regulators of mistletoe abundance and distribution.

Host Specificity

Mistletoes show wide variation in the degree of specificity in the host species they parasitize, both throughout their range and locally (Reid et al. 1995; de Lange et al. 1997). Some species parasitize a wide range of host trees, (e.g., *Lysiana exocarpi* and *Ileostylus micranthus*: Reid & Lange 1988; de Lange et al. 1997), whereas others exhibit a very high degree of host specificity (e.g., *Amyema gaudichaudii* and *Peraxilla colensoi*: Reid et al. 1995; de Lange et al. 1997). Some mistletoes have a wide range of hosts throughout their range but only parasitize a limited subset of host species locally (e.g., *Amyema miquelii*: Keneally 1973; Lamont 1985; Norton et al. 1995; N. Reid unpubl. data).

Pollination, Dispersal, and Infection

Mistletoe recruitment is dependent on a number of life-cycle steps associated with pollination, seedset, and successful dispersal to and establishment on a suitable host (Reid et al. 1995). Although insect pollination does occur in some species, most loranthaceous mistletoes in Australasia are bird-pollinated and exhibit varying degrees of specificity with avian pollinators (Bernhardt 1983; Ladley & Kelly 1995a,b). In areas with healthy pollinator and mistletoe populations, mistletoe seedset varies between 26% and 82% (Bernhardt 1983; Reid 1984).

Mistletoe establishment requires the successful dispersal of the diaspore to a suitable host branch and is dependent on an appropriate disperser, deposition on a suitably sized branch, and mistletoe-host compatibility. Specialist mistletoe dispersers are generally the most ef-

ficient and effective dispersers of loranth, but generalist frugivores may also successfully disperse undamaged diaspores (Reid 1991; Murphy et al. 1993; Ladley & Kelly 1996). Most mistletoe establishment occurs on small host stems, 3–20 mm in diameter (Reid 1991; Sargent 1995; Yan & Reid 1995). Establishment is also dependent on the genetic compatibility between the mistletoe seedling and its host, with significant variation in host susceptibility to mistletoe infection occurring at both the individual and population level (Reid et al. 1995).

Environmental Habitat Quality

Light and host water and nutrient relations are important determinants of mistletoe germination, establishment and growth. In viscaceous and loranthaceous mistletoes, percent germination is substantially greater in light versus dark, and some species only germinate in light (Lamont 1983). Mistletoe growth and fecundity may be higher in high light environments. Correlations have frequently been established between high mistletoe abundance and particular topographic situations, aspects and slopes, which may be related to light intensity (Hawksworth 1961). In New Zealand mistletoes appear to be most abundant at sites that have experienced either natural (e.g., snow break) or human (e.g., road edges) disturbance (B. Molloy personal communications) or in forests with structurally complex, heterogeneous canopies (Owen 1993).

Mistletoes have higher transpiration rates than their hosts (Ullman et al. 1985) suggesting that host water content may be an important determinant of mistletoe distribution and abundance. Studies in Australia and North America have shown enhanced mistletoe recruitment during or after periods of above average rainfall (Reid 1987; Dawson et al. 1990; Yan & Reid 1995). In central Australia higher densities of mistletoes are more likely to occur on host trees with higher foliage water content than on host trees with lower water contents (D. Norton & M. Stafford Smith unpublished data). Mistletoes are also dependent on the host xylem stream for nutrients, so profligate water use may be a means of maximizing nutrient gain (Ehleringer et al. 1985) or organic carbon (Marshall & Ehleringer 1990).

Predation

Invertebrates are important predators of mistletoes in Australia and New Zealand (de Baar 1985; de Lange 1997; Patrick & Dugdale 1997), although quantification of invertebrate impacts is limited. In the New Zealand mistletoe (*Peraxilla colensoi*), 3.4–4.7% of annual leaf loss was attributed to invertebrate browse (Owen 1993). Most predation appears due to Lepidopteran larvae (Kitching 1981; de Baar 1985; Platt & Edwards 1992), but predation by leaf and stem sucking insects such as

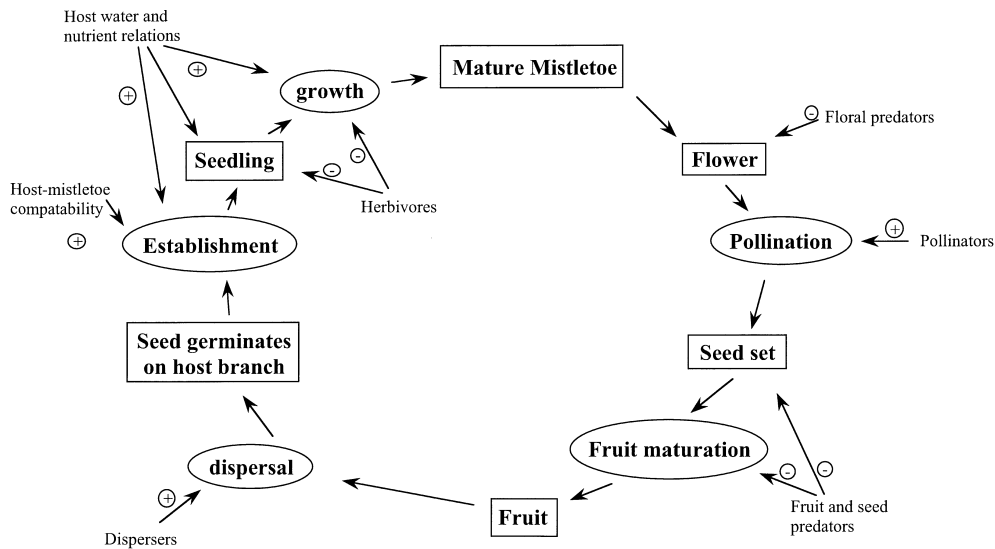


Figure 1. Important regulators and filters of mistletoe abundance and their point of action in the mistletoe life cycle.

scale and thrips is also widespread (de Lange 1997; N. Reid unpublished data). Main (1992) suggested that the decline in abundance of two mistletoe feeding butterflies in the Western Australian wheatbelt was due to decline in the abundance of mistletoes. Lepidopteran larvae and leaf-cutter ants also predate flowers, developing fruit and seeds in some Australian and Neotropical mistletoes (Reid 1987; Sargent 1995; N. Reid pers. obs.).

Mistletoe foliage and flowers are browsed by several arboreal marsupials in Australia including the brushtail possum (*Trichosurus vulpecula*), common ringtail possums (*Pseudocheirus peregrinus*), greater glider (*Petauroides volans*), and koala (*Phascolarctos cinereus*) (Young 1937; Campbell 1948; Henry 1985; Choate et al. 1987; Porter 1990; Evans 1992). Mistletoe foliage has also been documented in the diet of brushtail possums introduced into New Zealand forests (Owen & Norton 1995). Barlow and Wiens (1977) suggested that the evolution of mimicry in many Australian mistletoes had evolved in response to arboreal marsupial predation. Broad-tailed parrots (Platycercidae) are major pre- and post-dispersal seed predators of *Amyema* in Australia (Reid 1984; Yan & Reid 1995).

Disturbance

Natural disturbance regimes significantly affect mistletoe populations in many areas. Wildfire was a natural control agent of mistletoes in pre-European landscapes in both Australia (Turner 1991) and North America (Hawksworth 1961; Alexander & Hawksworth 1975). Some Australian mistletoes are fire-sensitive and are killed by complete leaf scorch (Kelly 1993). Drought may also reduce mistletoe populations (Reid & Lange 1988; Keast 1995). Disturbed sites are commonly associated with high light levels; forest edges and human-mod-

ified communities often have abundant mistletoes, and it has been suggested that mistletoes are opportunists in exploiting these disturbance dependent high light environments (B. Molloy personal communication).

Changes in Mistletoe Abundance in Australia and New Zealand

We hypothesize that the above evolutionary and ecological filters were the most important regulators of mistletoe abundance in pre-European landscapes in Australia and New Zealand (Fig. 1). With the arrival of Europeans the regulation of mistletoe abundance was modified by a series of changes in the existing environment or by the addition of new elements. These changes can be identified in the following three case studies.

Northern Tablelands Woodlands and Forests

Two mistletoe species (*Amyema miquelii*, *A. pendulum*) are significant parasites of eucalypts in the wooded pastoral landscapes of the Northern Tablelands of New South Wales (N. Reid, Z. Yan & C. Nadolny, unpubl. data). *A. miquelii* is particularly abundant in the region, infecting almost 50% of the large *Eucalyptus blakelyi* and *E. melliodora* trees along roadsides and in adjacent paddocks in some areas. A small percentage of such trees are heavily infested (>90% of canopy foliage consisting of mistletoe) and dead or dying eucalypts infested by *A. miquelii* or *A. pendulum* can be found. Reid (1995) argued that the present abundance of *A. miquelii* and, to a lesser extent, *A. pendulum* in the fragmented woodland and forest habitats of the Northern Tablelands is a function of at least three factors: reduced fire, de-

creased grazing and browsing, and increased habitat quality of remnant host trees.

The eucalypt woodlands and open-forests of the Northern Tablelands were subjected to frequent Aboriginal burning in pre-European times, with fire return intervals as high as 2–3 years (Norton 1971). Wildfire now occurs less frequently because of fire-suppression by landowners and bushfire brigades and because little hazard-reduction or range management burning occurs on the more intensively developed and heavily grazed properties.

Herbivore grazing and browsing pressure on mistletoes has decreased since European settlement due to the loss or decline of natural mistletoe predators. Common brushtail possums in particular were formerly abundant but declined due to heavy hunting pressure in the early part of the 20th century (Anon. 1945; Callister & Williams 1995). Numbers of the introduced fox (*Vulpes vulpes*) have increased in the past decade due to reduced hunting pressure for the fur trade, further reducing the numbers of brushtail possums (A. Smith, pers. comm.).

Fragmentation and tree removal, pasture fertilization, and road development may have increased the quality of remaining trees as mistletoe habitat by improving the moisture and nutrient status of scattered trees in paddocks and on roadsides, resulting in higher mistletoe establishment and growth rates. In open forests tree thinning may also lead to altered tree architectural patterns, with reduced abscission of lower branches due to increased light and reduced competition for moisture and nutrients, resulting in greater longevity and fecundity of mistletoe populations.

The projection of current trends for the Northern Tablelands is bleak for pest mistletoes, biodiversity conservation, and landscape productivity. In the absence of restorative management, tree cover will continue to decline because scattered tree populations in grazing lands are not regenerating due to livestock browsing (Reid et al. 1994). Roadside tree populations are regenerating, but pest mistletoes will continue to debilitate and kill these in the absence of burning and effective natural possum control. Ultimately pest mistletoe populations will decrease as tree cover declines to the point that pollinator and disperser populations also decrease; a number of bird species are already decreasing in abundance in these landscapes (Barrett et al. 1994). Agricultural productivity will also decrease as a result of increasing tree loss due to waterlogging, dryland salinization, and increased exposure (J. Prior, personal communication).

Wheatbelt Salmon Gum Woodlands

The Western Australian wheatbelt has experienced extensive habitat loss resulting in a highly fragmented landscape. Indigenous woodland trees are restricted to small

fragments, constituting only 7% of the original vegetation in some areas (Saunders et al. 1993). The scattered trees typical of the Northern Tablelands are not a feature of the wheatbelt because of widespread cropping. *Eucalyptus salmonophloia* is the dominant tree on heavier soils in valley floors and is infected by *Amyema miquelii*.

Habitat loss and disturbance to remaining fragments appears to be pushing *Amyema miquelii* toward extinction in the most modified areas (Norton et al. 1995), although it is common close to large tracts of unfragmented forest (Keneally 1973; Lamont 1985). In the most modified areas mistletoes are more abundant on average in larger fragments than smaller fragments, but small fragments either contain many or no mistletoes, reflecting the way in which fragmentation “samples” the pre-existing patchy distribution (Norton et al. 1995). The high mistletoe density in some ungrazed small fragments is reminiscent of the situation on the Northern Tablelands, but it appears that mistletoes will eventually be lost from these Western Australian fragments (Norton et al. 1995). Regional declines in key pollinating and dispersing bird species (Saunders 1993; D. Saunders pers. comm.) are likely to be an important cause of local mistletoe extinction. Reduced habitat quality in grazed fragments through changed water relations and removal of the shrubby understorey, an important food source for pollinating and dispersing birds (Cale 1990), also contributes to mistletoe decline (Norton et al. 1995). Without substantial habitat reconstruction (*sensu* Hobbs & Saunders 1993), it seems unlikely that *Amyema miquelii* will persist in the most modified parts of the Western Australian wheatbelt.

New Zealand *Nothofagus* Forests

Three mistletoe species (*Alepis flavida*, *Peraxilla colensoi*, *P. tetrapetala*) are almost exclusively parasites on *Nothofagus* (de Lange et al. 1997). Historical records suggest that these mistletoes were abundant in many *Nothofagus* forests at the end of the 19th century, but their range and abundance has declined markedly in several areas subsequently and they are now common only in southern and eastern South Island (de Lange & Norton 1997). Several factors account for their decline, but introduction of the common brushtail possum from Australia and loss of pollinating and dispersing birds are thought to be major factors (Ladley & Kelly 1995a,b, 1996; papers in de Lange & Norton 1997). A range of other factors has also been implicated including over-collecting (by botanists and florists), habitat loss, and predation by invertebrate pests and fungal pathogens (papers in de Lange & Norton 1997).

Brushtail possums were introduced to New Zealand to establish a fur trade and have become a major pest of indigenous plants and, to a lesser extent, indigenous ani-

mals (Cowan 1990). Experimental and empirical studies show a marked improvement in mistletoe vigor and condition with possum exclusion, whereas mistletoe decline in forests in which they were previously abundant is coincident with possum invasion (papers in de Lange & Norton 1997). However, the relationship between possums and mistletoes is not simple and availability of other foods modifies possum impacts on mistletoes (Owen & Norton 1995). Differences in architecture between mistletoe species also influences vulnerability and response to possum browse (Powell & Norton 1994).

These mistletoes appear to be strongly dependent on two honeyeaters (*Anthornis melanura* and *Prosthemadera novaeseelandiae*) for pollination and dispersal (Ladley & Kelly 1996; D. Kelly pers. comm.). For the two *Peraxilla* species, birds must physically open flower buds if cross-pollination is to occur (Ladley & Kelly 1995b). Local extinction or decline of these birds and other potential pollinators and dispersers has been suggested as a factor in the decline of beech mistletoes (Ladley & Kelly 1995a,b, 1996; Norton 1991).

It is likely that unless possum browse is reduced and predation of pollinating and dispersing birds stops, these mistletoes will continue to decline and become restricted to areas lacking these influences. Given the virtual absence of *Nothofagus* forest from off-shore islands that are possum and predator free, active management of possums and predators on mainland New Zealand will be necessary to sustain mistletoe populations.

Factors Leading to Current Mistletoe Status

Three broad groups of changes have led to the current status of mistletoes in the above examples.

Fragmentation

Tree thinning and fragmentation increase the nutrients and water available to remaining trees and therefore increase habitat quality for mistletoes. Fragmentation also negatively affects mutualists and predators (Ogle 1987; Bennett 1990; Saunders 1993; A. Smith pers. comm.). We hypothesize that at some point in tree-removal, the density of remaining trees becomes so low that mistletoe survival is negatively affected by loss of dispersers and pollinators and positively affected by loss of predators. Ultimately, tree clearance results in the local extinction of mistletoes through complete absence of hosts.

Neutral landscape models of *Amyema* mistletoes in fragmented landscapes show that at intermediate levels of tree clearing and constant numbers of host trees, mistletoe populations increase with increasing fragmentation (S. Lavorel, M. Stafford Smith & N. Reid, unpubl. data). Several studies have documented high mistletoe

abundances on isolated host trees in agricultural landscapes (e.g., Hartigan 1960; Calder et al. 1979; Ogle 1987). In Western Australia intense fragmentation has resulted in the almost complete loss of mistletoes from remnants in some areas (Norton et al. 1995), suggesting that the over-abundance of mistletoes predicted by Lavorel et al. (unpubl. data) will be short-lived if clearing continues beyond the tree density threshold that is capable of sustaining mistletoes and their mutualists.

Predation

Variation in predator abundance, especially herbivorous marsupials such as the common brushtail possum, is likely to affect mistletoe abundance in a predictable manner. Increases in predators in New Zealand (Wilson 1984; Ogle & Wilson 1985; Ogle 1997) and Australia (Young 1937) put mistletoes at a disadvantage, whereas reductions in predators have often been cited as a contributing factor to local mistletoe increase in Australian agricultural districts (Young 1937; May 1941; Serventy 1970).

Indirect or secondary impacts of predators on mistletoe abundance result from changes in the abundance of indigenous and naturalized predators following European settlement. Naturalized predators, especially *Rattus* species, mustelids (Mustelidae), cats (*Felis catus*), and foxes, have been introduced to Australia and New Zealand and have had major impacts on indigenous birds and mammals (Morton 1990; Bell 1991), including key pollinators, dispersers, and herbivores of mistletoes. These changes in vertebrate abundance have resulted in increases in mistletoe abundance in Australia through reduced herbivory and decreases in mistletoe abundance in New Zealand through loss of pollinators and dispersers.

Changes in Disturbance Regimes

Changes in fire regimes in Australian eucalypt woodlands and forests affect mistletoe abundance because mistletoes are more fire-sensitive than eucalypt hosts. After wildfire mistletoes rely on long-distance dispersal to reinvade whereas host tree populations have persistence mechanisms which enable burnt host trees to resprout or re-establish immediately after fire (Gill 1981). Most of the pre-European open-forests and woodlands that occurred in agricultural districts would have burnt frequently either as a result of wildfire or human activity (Gill et al. 1981). The post-settlement suppression of fire in agricultural districts permitted fire-sensitive mistletoes to increase (May 1941).

The secondary or indirect effects of altered disturbance regimes may also impact on mistletoe populations. In Western Australia disturbance through livestock grazing leads to increased soil compaction and decreased water infiltration in woodland soils (D. Norton

& R. Hobbs unpubl. data). The resulting reduction in tree moisture and nutrient status presumably reduces the quality of host trees as mistletoe habitat, contributing to the absence of mistletoes from grazed fragments (Norton et al. 1995). Similarly, the removal of understory from woodland and forest remnants in southern Australia reduces the nectar sources for pierid butterflies, which specialize on and sometimes defoliate *Amyema* mistletoes (Platt & Edwards 1992).

Conceptual Models of Mistletoe Abundance

Consideration of the way in which pre-European regulators of mistletoe abundance have been modified since European settlement allows us to develop conceptual models of the factors influencing the current status of mistletoes (Fig. 2). The models for each of the three examples are fundamentally similar although the intermediate outcome for mistletoe abundance varies. In each case Europeans caused two perturbations to the system—land clearance and biological invasion—resulting in direct and indirect cascading effects on the regulators of mistletoe abundance in pre-European landscapes. These changes have, in turn, resulted in either increases or decreases in mistletoe abundance that are symptomatic of a more general deterioration in ecosystem condition within each of the areas. Even on the Northern Tablelands, where mistletoes are increasing, this effect may be transitory and the long-term prognosis suggests that without active ecosystem management, mistletoes will ultimately face local extinction in these systems as well. Decline in ecosystem condition will be characterized in all three examples by loss of indigenous biodiversity, and, in the two Australian examples, loss of agricultural productivity as well.

Managing Mistletoes through Ecosystem Management

For many reasons land managers often react to pest or threatened species problems with therapeutic solutions designed to treat symptoms rather than adopting preventative solutions that address underlying causes. On the Northern Tablelands effective control of pest mistletoes is achieved by pruning, pollarding, or burning infected trees (Reid et al. 1994; Reid 1995) or by stem injection with chemicals (Minko & Fagg 1989). In New Zealand *Nothofagus* forests short-term approaches have involved banding of individual host trees and caging of individual mistletoe plants to prevent possum browse (de Lange & Norton 1997). These approaches are only effective in the short-term, are expensive to apply over large areas, and will be prohibitively expensive in the long-term and on a broad scale.

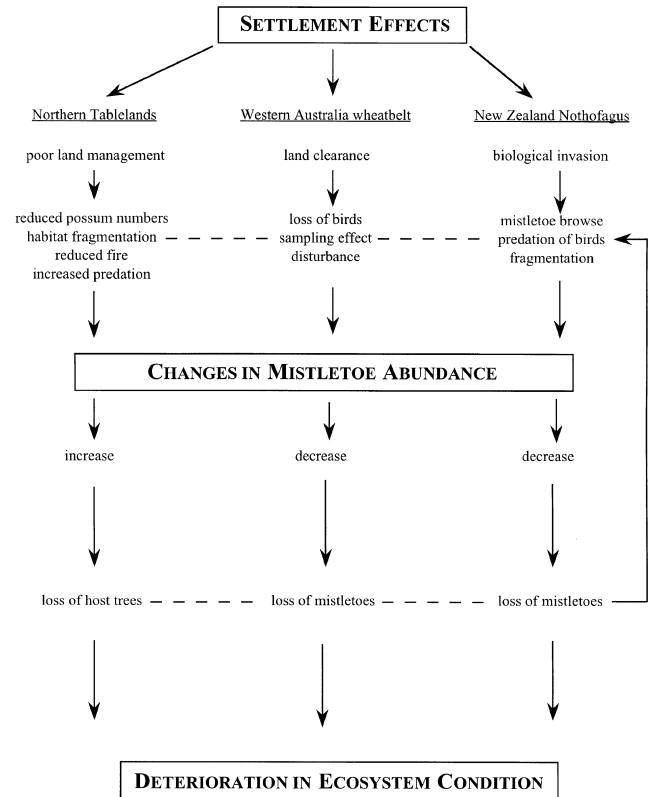


Figure 2. Models of altered mistletoe abundance brought about by impacts of European settlement in Australia and New Zealand.

Long-term solutions need to address the underlying causes of the problems facing mistletoes; they need to be preventative and emphasize ecosystem management principles, that is management of the different components or factors that directly or indirectly influence mistletoe abundance. In each of the examples mistletoes are either increasing or decreasing due to more than one impact of European settlement, so addressing only one impact will not necessarily solve the problem. For example, in Australia, grazing management to permit natural regeneration and survival of paddock tree populations in the long-term does not address the problem of high fox numbers or overzealous land clearance in the past, both of which are contributing to the extinction of possums over much of their former distribution. Based on these considerations, we suggest the following ecosystem-based approaches for managing mistletoes in the three example areas.

On the Northern Tablelands of NSW, long-term solutions need to maintain mistletoes at sustainable intermediate levels of abundance, thereby maintaining ecosystem health. Grazing management, pasture fertilization, and cultivation practices need to be modified to permit the persistence and regeneration of paddock trees in grazed

landscapes. Extensive, integrated fox and rabbit (*Oryctolagus cuniculus*) control will need to be undertaken to allow brushtail possum populations to recover without permitting an explosion in rabbit numbers when fox predation is eased or indirectly targets possums in error. Recovery of possums and other natural control agents such as rosellas and mistletoe-specializing insects will also require the extensive use of catchment and whole-farm planning so that wildlife corridors and ungrazed remnants with appropriate understory species and adequate tree hollows are preserved across the landscape, and are integrated into land management strategies for agricultural production on private land. In some areas prescribed fire and other short-term control measures may still be required to periodically check the increase of local infestations of pest mistletoes.

The Western Australian wheatbelt has experienced such substantial changes that the only realistic option for management is restoration of whole ecosystems (Hobbs & Saunders 1993). Without such an approach it seems unlikely that mistletoes will persist naturally without continuing reintroduction efforts. Restoration must focus on quality habitat for both mistletoes and pollinating and dispersing birds and will need to include consideration of both grazing impacts on habitat quality (Norton et al. 1995) and the provision of adequate alternative foods for key pollinators and dispersers (Lambeck & Saunders 1993). Active reintroduction of mistletoes, their pollinators and dispersers, and other habitat elements of the birds (e.g., other food plants) will be necessary to restore ecosystems. As with the Northern Tablelands, consideration will need to be given to integrated fox and rabbit control.

Long-term management solutions to the decline of mistletoes in New Zealand *Nothofagus* forests must address both direct herbivory by possums and the effects of various predators (especially rats and mustelids) on key pollinating and dispersing birds. Addressing one in isolation will not result in long-term benefits for mistletoes or for overall ecosystem condition. Integrated pest control will need to involve several pest species at a site (e.g., Saunders 1990). Given the large area requirements of mobile bird populations and the patchy nature of mistletoes, such control areas will need to be large. With currently available technology, this will require intensive continuing integrated pest management to "hold the line" until new technologies (e.g., genetic engineering) allow more effective and efficient control. In *Nothofagus* forests where mistletoes have now largely been lost (e.g., northwestern South Island and North Island), active reintroduction of mistletoes will be necessary. Habitat loss is no longer a significant issue for most areas with these mistletoes because most forests in New Zealand are now managed for nature conservation.

A similar ecosystem-wide (or "holistic") approach to problem-solving is advocated by land managers in other

resource management disciplines. For example, in the rangelands of the southwestern U.S.A, native populations of mesquite (*Prosopis* spp) have invaded prairie vegetation in historical times, reducing livestock production. An integrated brush management framework involving grazing management, use of fire, diversification of land-use objectives and productive enterprises, and short-term control solutions is advocated to maintain an ecological and economic balance between various land uses and landscape vegetation states (Holechek et al. 1989).

Conclusions

Six main implications can be drawn from the mistletoe examples we have presented in this paper:

- (1) It is not possible to manage mistletoes either as pest or threatened plants in the long-term without considering their ecosystem context.
- (2) To manage mistletoes it is essential to understand the factors that regulated mistletoe distribution and abundance prior to European settlement as well as the factors that have modified these regulators more recently. Without understanding these regulators and modifiers, it is not possible to identify the ecosystem processes that are essential for mistletoe management.
- (3) The current (pest or threatened) status of mistletoes is not the result of a single direct impact of European settlement. Rather, several factors are involved, including indirect, cascading, trophic effects involving "third-party" organisms in addition to the mistletoes, their mutualists, and predators.
- (4) The examples provide a predictable contrast between systems involving two organisms (mistletoes and possums) where in one system, the mistletoes are threatened by proliferation of possums (New Zealand), and in the other system mistletoes increase in abundance because of declining possum numbers (Northern Tablelands).
- (5) In the case of *A. miquelii*, which is both declining and a pest in different parts of Australia, the resource management information needed to effectively manage this species in the long term is different in the two situations. In the Western Australian case where the mistletoe is declining, management requires information on dispersers (and perhaps pollinators), habitat fragmentation, and grazing impacts on remnant woodlands. On the Northern Tablelands where the mistletoe is a pest, information is needed on fire, grazing and pasture management, native herbivores, and introduced carnivores. However, despite the particular information needs, broad ecosystem management solutions are ultimately required in both cases.

- (6) In the two Australian examples the management required for successful mistletoe conservation cannot preclude productive use of the same landscapes. Rather, because of the preponderance of land in private ownership, long-term conservation of mistletoes requires integrated management encompassing the needs of both conservation and sustainable agricultural production.

Although we now have considerable information on which to base the ecosystem management of mistletoes, there are still critical knowledge gaps. Birds are a key component of mistletoe ecology, yet we know little about their movement patterns at the landscape scale and how this influences mistletoe distribution patterns. There is increasing evidence for a genetic basis to the success of mistletoe establishment on host plants (Reid et al. 1995) which requires further study. Such research has important implications for management program involving introduction of non-susceptible host trees (in Australia) or introduction of mistletoes to new (safe) sites (in New Zealand). The mistletoe-host relationship also requires further investigation with respect to habitat quality (e.g., host tree size and nutrient and water status). Finally, the reality of modern ecosystems in Australia and New Zealand is that we may not be able to eliminate exotic species in the near future and key predators such as foxes, possums (in New Zealand), stoats, and rats are likely to be part of mistletoe ecosystems in the short to medium term. A key question is what levels can these predators occur without causing unwanted decreases or increases in mistletoe abundance?

The problems facing mistletoes documented here are unusual because of the complexity of the interactions involved. Although changes in the abundance of one group of organisms in response to changes in a second have been widely documented (pollination and dispersal mutualisms and predator-prey relationships), there are few documented examples of higher-order interactions similar to those here (but see Norton et al. 1997). It is unlikely that mistletoes are unique in this respect and it is important that conservation biologists and managers are aware of the potential occurrence of more complex interactions.

Although short-term solutions may be critical to the immediate survival of threatened taxa or the short-term control of burgeoning pest populations, long-term solutions couched in an ecosystem management framework will be ultimately critical to maintenance of the mistletoe populations reviewed here and, we suspect, to the majority of the world's biodiversity. In productive landscapes ecosystem management approaches to biodiversity conservation will have to involve integrated landscape management to preserve both the private and public utility of land (Hobbs & Saunders 1993).

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