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Survival and Recolonisation of Australian Mistletoes after High Severity Fire: Implications for the Warrumbungle National Park

Cameron William Kirk

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Survival and Recolonisation of Australian Mistletoes after High Severity Fire: Implications for the Warrumbungle National Park

Abstract

Fire events in south-eastern Australia are increasing in frequency and severity resulting from climate change. The existing fire adaptation research for Australian flora has focussed on fire adapted lineages. However, it is important to understand the dynamics of fire vulnerable species and the mechanisms by which they persist in fire-prone environments. Mistletoes are an example of a fire vulnerable species that lacks the ability to resprout or reseed, relying on recolonisation following fire. This thesis furthers fire ecology by establishing a relationship between fire severity and the survival of mistletoes through the 2013 Wambelong fire in the Warrumbungle National Park. It was expected that high severity fire would eliminate mistletoe populations. This thesis also sought to identify the effect of mistletoe height, size, host fire health, host species, and ecological community mistletoe survival. It assessed this relationship through 81 transects across a diverse array of fire severities. The thesis identified a baseline survival rate of 69.4% for unburnt regions. High severity exhibited a corrected survival of 0.351%, showing a dramatic decline in mistletoe survival. Mistletoe size, host fire health, host species and host community all exhibited significant effects on mistletoe survival. Contrary to assumptions, mistletoe height did not exhibit an effect on mistletoe survival. The thesis showed that high severity fire played an important role in determining mistletoe distribution. The findings suggest that mistletoes use edge recruitment to recolonise after high severity fire and may require a multi-decadal fire-free period or risk to recover at a landscape level.

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Survival and Recolonisation of Australian Mistletoes after High Severity Fire: Implications for the Warrumbungle National Park

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University of Wollongong

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A thesis submitted in partial fulfilment of the requirements of the Bachelor of Environmental Science (Honours) in the School of Earth, Atmospheric and Life Sciences, Faculty of Science, Medicine and Health, University of Wollongong, 2022

I would like to begin this thesis by acknowledging the traditional custodians of the Warrumbungle National Park, the peoples of the Kamaroi, the Wiradjuri, and the Weilwan. I would like to pay my respects to their elders, past, present, and future.



Figure i. A White Box found infested with about 30 different Drooping Mistletoe individuals, found near Wambelong Canyon Campground. A small but strong community of mistletoes surrounded predominantly by the moderate to high fire severity areas that brought the mistletoepocalypse. *Feat* Andrew Denham, Senior Research Scientist, Department of Planning and Environment. Image Credit: Cameron Kirk (2022)

The information in this thesis is entirely the result of investigations conducted by the author, unless otherwise acknowledged, and has not been submitted in part, or otherwise, for any other degree or qualification.

Signature:

Date: 9th of November, 2022

I would like to acknowledge the Department of Planning and Environment for inspiring and facilitating this thesis. You have provided the means for me to contribute to a research program far larger than any one individual could tackle. It has been an exceptionally interesting topic question in an area I likely never would have learned about. I hope this research has thoroughly addressed the questions you sought to answer and will inform research and management decisions to come.

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Cheers to you champions, I couldn't have done it without you

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Abstract:

Fire events in south-eastern Australia are increasing in frequency and severity resulting from climate change. The existing fire adaptation research for Australian flora has focussed on fire adapted lineages. However, it is important to understand the dynamics of fire vulnerable species and the mechanisms by which they persist in fire-prone environments. Mistletoes are an example of a fire vulnerable species that lacks the ability to resprout or reseed, relying on recolonisation following fire.

This thesis furthers fire ecology by establishing a relationship between fire severity and the survival of mistletoes through the 2013 Wambelong fire in the Warrumbungle National Park. It was expected that high-severity fire would eliminate mistletoe populations. This thesis also sought to identify the effect of mistletoe height, size, host fire health, host species, and ecological community mistletoe survival. It assessed this relationship through 81 transects across a diverse array of fire severities.

The thesis identified a baseline survival rate of 69.4% for unburnt regions. High-severity exhibited a corrected survival of 0.351%, showing a dramatic decline in mistletoe survival. Mistletoe size, host fire health, host species and host community all exhibited significant effects on mistletoe survival. Contrary to assumptions, mistletoe height did not exhibit an effect on mistletoe survival. The thesis showed that high-severity fire played an important role in determining mistletoe distribution. The findings suggest that mistletoes use edge recruitment to recolonise after high-severity fire and may require a multi-decadal fire-free period or risk to recover at a landscape level.

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Chapter 1. Introduction:

1.1 General Introduction

Fire is a powerful disruptive force that is prevalent in the Australian environment. It acts as a filter that determines the spatial patterns and dynamics of plant communities (Prior & Bowman 2020). It has been suggested that fire has been a driving force in the evolution of Australian biota for at least 61 million years, when the modern fire-adapted lineages appear in the fossil records (Lamont & He 2012). Many plants have evolved adaptations that allow them to persist through fire, including resprouting through epicormic buds or reseeding through persistent seed banks (Barker et al. 2022; Burrows 2013). Despite this, some plants do not exhibit traits to persist through fire events and rely on colonisation to re-establish after fire (Prior & Bowman 2020). As the frequency and severity of fires continue to increase in Australia as a result of anthropogenic climate change (Clarke, H et al. 2013) it is becoming increasingly important to understand how these fire vulnerable coloniser species can persist in a fire prone landscape. Mistletoes are an excellent example of a fire vulnerable coloniser, lacking any form of seed bank and cannot resprout after fire (Gosper & Prober 2020). Because of this, they may be among the most vulnerable flowering plants in Australia to the changing fire regimes.

Mistletoes are a functional group of plants characterised by an aerial hemi-parasitic habit. (Barlow 1983; Watson 2019). As aerial hemi-parasites, mistletoes typically grow in the canopy or on the branches of the trees that they parasitise, having no underground root systems of their own. In contrast to true-parasites, hemi-parasites like mistletoes do not rely solely on their host for energy (Scalon & Wright 2017). Mistletoes are photosynthetic plants that draw the required nutrients and water for photosynthesis from the xylem stream of a host plant through a modified root known as a haustorium (Scalon & Wright 2017). Once the haustorium is established, the mistletoe draws the water and nutrients from the host through a high transpiration rate (Fisher 1983) and high concentration of cations (Crates et al. 2022) that creates a large pressure gradient in favour of the mistletoe (Scalon & Wright 2017). The hijacked xylem network will no longer deliver nutrients and water to the branch further along from the mistletoe leading to its death (Watson 2019).

Mistletoes have a complex interdependencies and relationships with other plants and a wide variety of vertebrate and invertebrate animals that make them important ecological resources (Watson 2019; Watson & Herring 2012). Their flesh provides an important source of food for frugivorous birds and bats, folivorous insects and mammals and pollinating insects (Anderson & Braby 2009; Braby 2006; Watson 2019; Watson & Herring 2012). Their nutrient rich litterfall enriches the understory (*March & Watson 2007*) and they provide an important nest substrate for a wide variety of bird species (Barea 2008; Cooney & Watson 2008; Cooney et al. 2006). While many bird species opportunistically feed on mistletoes, Australia is home to two species with a diet consisting almost entirely of mistletoe fruit

(Reid 1989; Roxburgh 2007; Walsberg 1975). This relationship with birds is mutualistic as the mistletoe relies on frugivorous birds to disperse its seeds to uninfected hosts (Watson 2013, 2019). It is because of these interdependencies that mistletoes have been proposed as keystone species (Watson 2001), supported by their disproportionate effect on avian biodiversity (Watson & Herring 2012).

Mistletoes are all members of the Santalales order, divided into 5 families categorized by the 5 independent evolutions of the aerial parasitism trait (Watson 2019). Mistletoes in Australia represent two of these families, Loranthaceae and Viscaceae (Watson 2019). Loranthaceae is the most dominant family of mistletoes in Australia. Loranthaceae mistletoes had a widespread distribution across the Australian landmass prior to its separation from Gondwana (Barlow 1983). Viscaceae makes up a much smaller group of mistletoes in Australia, having radiated to Australia across the narrow straight between the Sunda landmass of South-east Asia and the Sahul landmass of Papua-Australia during the Miocene (Barlow 1983).

Australia is a continent that is regulated by a prevalent regime of fire. Despite constituting 5% of the global terrestrial area (Geoscience Australia 2004), Australia accounts for an average of 13% of the annual global fire affected area (Giglio et al. 2013). The climate of subtropical Australia is dominated by dry, clear weathers with hot summers that promote fire conditions (Lindsey 2003). The fire conditions are exaggerated by large scale climatic oscillations that create extended periods of high precipitation that promotes rapid fuel growth, and extended periods of high temperature and low precipitation that promotes fire conditions (Sullivan et al. 2012). The fire regime of Australia evolved as the continent dried during the Oligocene (Hopper & Gioia 2004; Rundel et al. 2016). This led to the radiation of fire-loving sclerophyll forest (Hopper & Gioia 2004; Rundel et al. 2016). By the Holocene, fire had become common across all Australia biomes except for isolated rainforest sanctuaries (Pyne 2017).

Loranthaceae mistletoes have been present since the separation of Australia from Gondwana, evolving alongside this changing regime of fire. Despite this coevolution with fire, only a select few species of Australian mistletoes have been shown to display strategies that allow them to survive in fire-prone environments (Start 2011). The manual application of fire has been an effective tool in removing mistletoe infections in forestry plantations for both Loranthaceae (Kelly et al. 1997) and Viscaceae (Shaw et al. 2004). Mistletoes have shallow epicormic buds present in the stem and haustorium that is killed instantaneously when tissue temperature reaches 64°C (Kelly et al. 1997). This means that higher severity fires likely kill all mistletoes and suggests low severity ground fires would create sufficient conditions to scorch mistletoes growing close to the ground (Kelly et al. 1997; Watson 2019).

Fire severity is a metric used to classify the ecological impact of a fire on the ecosystem (Gordon, Price & Tasker 2017; Keeley 2009). In Australian Eucalypt forests it is used to represent the consumption of biomass by the fire in a vertical frame of reference (Etchells et al. 2020; Palmer et al. 2018). It is

typically determined through one of several proxies including tree mortality (Keeley 2009), foliage loss or destruction of terminal branches (Dickinson & Johnson 2001; Moreno & Oechel 1989; Tolhurst 1995), change to soil chemistry (Neary et al. 1999; Wells et al. 1979), and visual changes for remote sensing techniques (Chafer et al. 2004; Gordon, Price & Tasker 2017; Veraverbeke et al. 2011). Fire severity is broken up into different qualitative severity categories; unburnt, low, moderate, high, (Chafer et al. 2004; Gordon, Price & Tasker 2017). Some papers will also include an extreme category above high severity (Gibson et al. 2020). Each category represents the degree of vegetation change: low severity represents an understory fire, moderate severity represents a partially scorched canopy, high severity represents full canopy scorch, and extreme severity represents a complete canopy consumption (Gibson et al. 2020).

1.2 The Warrumbungle National Park

The Warrumbungle National Park [WNP] encompasses 23312 hectares in the central north of New South Wales, located 33km west of the nearest town Coonabarabran (NSW National Parks and Wildlife Service [NPWS] 2012). The mountainous national park exists on the remnant of a shield volcanic complex (Bull et al. 2020) that acts as the boundary between the Pilliga sub-region of the Brigalow Belt South Bio-region and the Darling Riverine Plain Bio-region, attracting a wide variety of flora and fauna from both bio-regions (NPWS 2012). The park hosts a large number of protected or vulnerable plant (Hunter 2008a) and animal species (NPWS 2012); including the Regent Honeyeater, a critically endangered species of concern to the Department of Planning and Environment that relies primarily on mistletoes for nectar and nest substrates (Oliver 2000; Thomas 2009).

At 4pm on the 12th of January 2013, a small fire was reported to the NSW Rural Fire Service near the Wambelong Camping Area in the WNP (Brown et al. 2015). Within 24 hours it was declared the highest category of wildfire with catastrophic fire conditions promoting rapid fire expansion (Murphy 2013). The main fire was extinguished on the 24th of January (Murphy 2013) but spot fires would continue to burn until the 21st of February (Brown et al. 2015). It was the first catastrophic wildfire in the WNP since 1967 which burned 95% of the WNP (Brown et al. 2015). 72% of the burned area within the WNP was at moderate to high severity (Tulau et al. 2019; Yang et al. 2018). The fire caused intense damage to nearby farms and properties, destroying 184 buildings and killing over 1000 livestock (Murphy 2013). The fire caused significant alterations to the vegetation structure of the WNP (Denham et al. 2016; Gordon, Price, Tasker, et al. 2017). In addition, fire vulnerable species within the park may suffer extirpation from a subsequent fire, potentially requiring a fire-free period exceeding 30 years to reduce this risk (Denham et al. 2016). Because of this, the Department of Planning and Environment has funded numerous research and rehabilitation projects to understand and minimise the effects of large fire events.

1.3 State of Research

The primary literature regarding the interactions of Australian mistletoes and fire is extremely limited. The largest source of related information comes from North America where several studies have assessed the viability of using fire to control the spread of *Arceuthobium*. *Arceuthobium* are a Viscaceae genus known as dwarf mistletoes that parasitises commercial coniferous species and are extremely detrimental to the health of the host (Shaw et al. 2004). However, research suggests that dwarf mistletoes are not a good analogy for Australian mistletoes despite their similar biology (Shaw et al. 2004). A similar study into the manual application of fire as a treatment for *Amyema* mistletoes in Australian Eucalypt plantations has shown that short (>20s) exposure to fire is an effective control for mistletoes (Kelly et al. 1997). Four studies have assessed the effects of wildfire on Australian mistletoes. However, the studies do not assess the effect of fire severity, but rather assess the effect of historic fires on mistletoe distribution and biodiversity, and the survival strategies used by mistletoes to survive and recolonise (Gosper & Prober 2020; Start 2011, 2013, 2015). These studies have been conducted in Western Australia which is subject to different fire regimes and mistletoe assemblages to south-eastern Australia.

This presents an opportunity to further the research and understanding regarding the interactions of Australian mistletoes with fire severity in south-eastern Australia. It is important for management and rehabilitation practices to understand the strategies plants use to persist in fire prone landscapes as it is a dominant ecological disturbance present in almost all Australian biomes. Due to the high level of interdependencies mistletoes have with animals it is also important to understand mistletoe management as a resource to protect and manage declining, vulnerable, and endangered species that rely on mistletoes for food or habitat.

1.4 Purpose of the Thesis

This thesis is intended to inform the Department of Planning and Environment on the effect of the Wambelong fire on the mistletoe populations of the Warrumbungle National Park. It addresses a gap in the literature regarding the interactions of mistletoes and fire severity in a fire regime typical of inland south-eastern Australia. This thesis aims to assess the effect of fire severity on the survival rate of mistletoes within the WNP. This will be used to develop a model for dry sclerophyll forest to predict the survival rate of mistletoes as a function of fire severity. In addition, the effect of host fire health rating will be assessed to determine the difference between field and remote methods. It is hypothesised that:

1. Mistletoe survival rate will decrease with increasing fire severity
2. Mistletoe survival rate will decrease with increasing host fire health rating

This thesis will also address additional variables that may influence the survival rate of mistletoes following fire events. This includes the effect of the mistletoe characteristics: height, measured from the haustorium to ground level, and mistletoe size estimated from vertical and horizontal extent. This also includes the effect of biotic factors including host species, and host ecological community. It is hypothesised that:

3. Mistletoe survival rate will increase with increasing mistletoe height
4. Mistletoe survival rate will increase with increasing mistletoe area
5. Mistletoe survival rate will vary between host species
6. Mistletoe survival rate will vary between host ecological communities

Chapter 2. Literature Review:

As the existing research into the effects of fire on Australian mistletoes is a highly fragmentary field of literature, this chapter will provide a broader selection of literature aimed to provide the background context for an in-depth analysis into a relatively emergent field of Australian ecology. The focus of this literature review regards the biology and ecological interactions of Australian Loranthaceae mistletoes, the characteristics, regimes, and driving forces of fire in south-eastern Australia, and the ecology of the Warrumbungle National Park.

2.1 Australian Mistletoes

The term mistletoe is broadly used to describe a polyphyletic taxonomic group of shrubby, wooded plants that have developed an aerial-parasitism habit on a host plant (Barlow 1983; Watson 2019). Mistletoes are partial or hemi-parasites that obtain water and mineral nutrients from the host plant while producing sugars through photosynthesis (Calder 1983). Mistletoes are restricted to five families within the Sandalwood (Santalales) order including: Christmas or ‘true’ mistletoes (Viscaceae), showy mistletoes (Loranthaceae), feathery mistletoes (Misodendronaceae) and two families in the Sandalwood complex (Amphorogynaceae & Santalaceae) (Watson 2019). Not all members of these families follow the definition of a mistletoe, including *Nuytsia floribunda* ‘Western Australian Christmas Tree’ and *Atkinsonia ligustrina* ‘Atkinsonia’, which are both Australian Loranthaceae that display a terrestrial root parasitism habit (Calder 1983; Watson 2019). Conversely, not all plants that display an aerial-parasitism habit are considered mistletoes (Calder 1983; Watson 2019). As of 2019, the Australia continent has members from 3 of the 5 mistletoe families, including 97 identified species of mistletoe (Watson 2019). Of the 97 species, 71 are endemic to the Australian continent while 26 are distributed through South-East Asia and Oceania; including New Guinea, New Caledonia and the Philippines (Watson 2019).

Loranthaceae is the dominant family of mistletoes in Australia, accounting for 80 of the 97 endemic species of mistletoe as well several species of root parasitic shrub (Watson 2019). Barlow (1983) attributes the dominance of Loranthaceae to the paleogeographic history of Australia. They theorise that Loranthaceae had achieved a wide distribution across the paleo-continent of Gondwana by the mid-Cretaceous, where it had already experienced significant diversification in morphology and distribution. Barlow (1983) also theorises that the Sunda arc-system would have allowed the two-way migration of Loranthaceae between the Sunda landmass (modern day Borneo, Java, Malay Peninsula, and Sumatra) and the Sahul shelf (modern day Australia and Papua New Guinea) during the Miocene. This allowed mistletoe stocks from the Indian-Gondwanan fragment to spread back across the floral corridor to Australia. Loranthaceae is found in almost all wooded habitats in continental Australia, having achieved a widespread distribution in hosts and climate through its species (Watson 2019). Viscaceae is the next

most dominant family of mistletoes, accounting for 17 species of mistletoe in Australia (Watson 2019). None of the Viscaceae species are endemic, having a wider distribution beyond Australia (Watson 2019). Viscaceae is a newer family of mistletoes, having achieved a widespread distribution across the paleo-continent of Laurasia during the Palaeocene and spreading to Australia from the Asian continent through the floral corridor between the Sunda and Sahil landmasses (Barlow 1983). The distribution of Viscaceae is severely limited in Australia, restricted primarily to the wetter habitats found in Eastern Australia and Far-North Queensland (Watson 2019). Only four known species of Viscaceae have crossed the great dividing range, with only two known to have dispersed as far as South Australia and Western Australia (Watson 2019). They primarily parasitise rainforest trees but can parasitise other mistletoes which suggests a much wider distribution of Viscaceae is possible than what is observed (Watson 2019). The final mistletoe family in Australia is Amphorogynaceae, which is only represented in Australia by several species of root parasitic shrub and does not have any aerial habit mistletoes (Watson 2019). Due to the limited dispersion of Viscaceae and Amphorogynaceae, this thesis will focus primarily on the Loranthaceae family of mistletoes.

2.1.1 Biology of Loranthaceae

Loranthaceae mistletoe begin their lifecycle as a pseudo-berry, a type of fruit characterized by the absence of true ovules (Bhatnagar & Johri 1983; Calder 1983); with exception of two root parasitic genus, *Atkinsonia* and *Gaiadendron*, which both display pseudo-drupe type fruits (Bhatnagar & Johri 1983). In mistletoes, the fruit predominantly contains a single embryo surrounded by endospermic tissue and pericarp (Calder 1983). At the maturity of the berry, the pericarp shows four distinct zones: an outermost leathery rind; a viscid layer; a fleshy zone; and a vascular zone (Bhatnagar & Johri 1983) displayed in figure 1. The outermost leathery rind occupies approximately half of the width of the pericarp (Bhatnagar & Johri 1983). The viscid layer varies greatly between Loranthaceae members (Bhatnagar & Johri 1983), but is characterized by elongated and diagonally placed cells that secret viscin (Singh 1952). The viscin is a sticky translucent pulp that aids in the attachment of the seed to a the bill, plumage and feet of dispersers (Liddy 1983), and host substrates (Watson 2019). It also provides a source of moisture for the embryo within, capable of rehydration in contact with rain or dew (Watson 2019). The viscid layer is divided into two regions, the outer layer is easily digestible by birds while the inner layer remains unaffected by bird digestive systems (Bhatnagar & Johri 1983). The fleshy zone consists only of vertically elongated cells containing tannins, with exception of the root parasitic members which display an additional sclerotic zone (Bhatnagar & Johri 1983). The vascular zone comprises of parenchymatous cells and acts to supply the floral organs (Bhatnagar & Johri 1983).

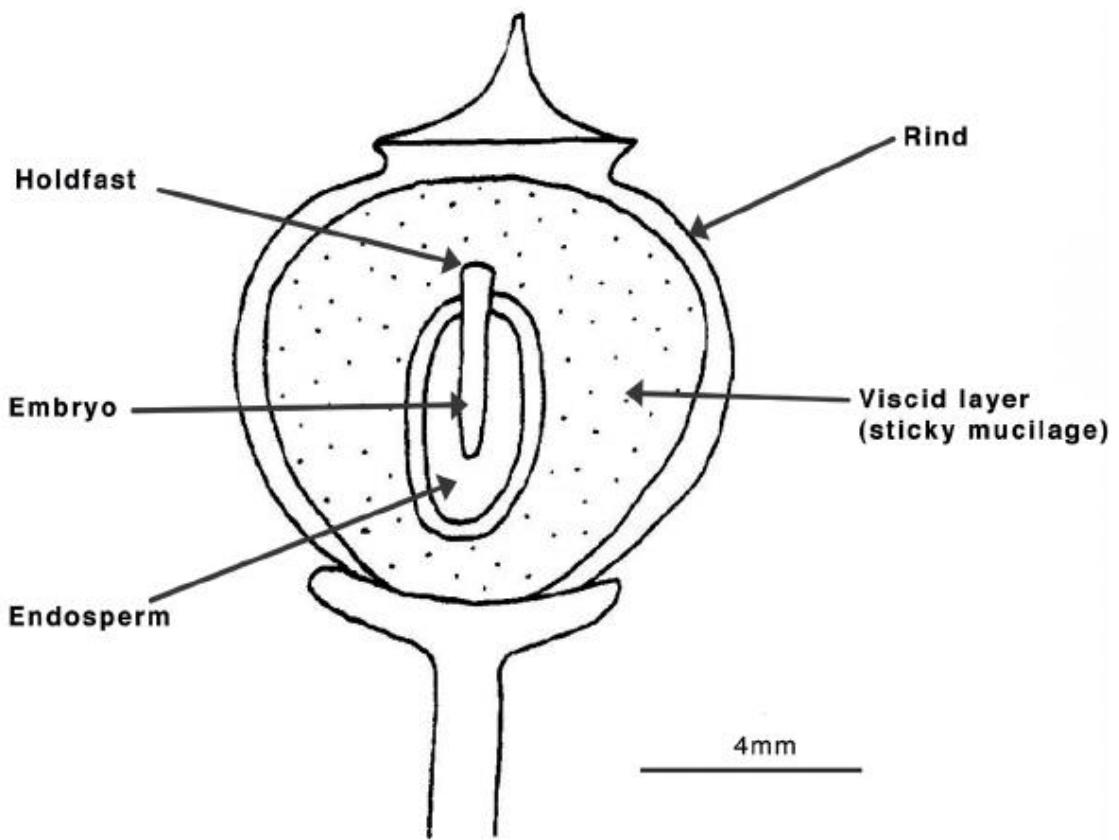


Figure 1. Diagram of a longitudinal cross section through a mature *Amyema* (Loranthaceae) pseudo-berry showing the rind and viscid layer. Image by Groom and Lamont (2015)

Germination of the seed will trigger as soon as the fruit rind is breached upon removal from the plant (Watson 2019). Studies show a high germination rate for Loranthaceae that is independent of the site of deposition (Watson 2019). Almost all seeds consumed by birds will germinate, with studies showing that up to 97% of seeds defecated by Mistletoebirds will germinate (Liddy 1983). Similar patterns are observed in seeds eaten by Orioles, Lewin's Honeyeaters, and Silvereyes, which all displayed 100% germination rate (Liddy 1983). However, the sample population presented by Liddy (1983) is small for non-Mistletoebirds. Despite the high germination rate observed for bird defecation, seed germination will occur without consumption (Lamont 1983). As seeds germinate independent of location they will readily germinate on unsuitable substrates such as fence posts, powerlines, or dead hosts (Watson 2019). Seeds that establish on unsuitable substrates will adhere via the holdfast and can survive for six months, but further growth cannot occur without a host connection (Watson 2019). The external sources of nutrients and water that germinating autotrophic species rely on are unavailable to germinating mistletoes until the host connection is established (Lamont 1983). Seeds rapidly germinate and establish a haustoral connection (Lamont 1983) to source the water and nutrients required for photosynthesis (Watson 2019). Further risks during the germination stage endanger the mistletoe seed including dislodgement, exposure, and predation (Lamont 1983). Unlike many terrestrial species a large number of mistletoes will readily germinate in dry air (Lamont 1983). Humidity may decrease the

survival rate of germinating Loranthaceae seeds based on early botanic studies on *Viscum album* (Viscaceae family) that showed 90% humidity causes mass seed rot (Lamont 1983; Wiesner 1897); though this effect has not been verified for Loranthaceae. Mortality due to rot has been observed on Australian Loranthaceae seeds due to high precipitation and frost (Lamont 1983). Additionally, as mistletoe seeds germinate on removal they do not form seedbanks (Reid et al. 1995).

For a germinated seed to establish it must form a connection to the host plants vascular system. A fused tube-like cotyledon rapidly grows out from the seed towards the attached substrate (Watson 2019). The cotyledon penetrates the host bark through a combination of mechanical force and enzymatic digestion to form a holdfast (Watson 2019). Once the connection has been made the cotyledon will unfold and shed the outer skin (Watson 2019). The connection point between the mistletoe and the host is a modified root called a haustorium (Kuijt & Lye 2005; Scalon & Wright 2017; Watson 2019) where haustoria, sinker like outgrowths, penetrate the host and make a connection with host xylem (Fisher 1983). The thickness of the bark of the branch is important in establishing the mistletoe, typically for Australian mistletoes branches thicker than a pencil will be impenetrable to the mistletoe (Watson 2019). Once xylem to xylem contact has been established water and nutrient flow begins and will not be disrupted (Fisher 1983). Haustoral organs of parasitic organisms, especially within Loranthaceae, is a poorly understood field of research (Fisher 1983; Kuijt & Lye 2005) with exception of three well studied species: *Nuytsia floribunda*, a root parasitic mistletoe from Western Australia (Fineran & Hocking 1983); *Tristerix aphyllus*, a specialised mistletoe that parasitises cactus in South America (Mauseth 1990); and *Psittacanthus ramiflorus*, a neo-tropical mistletoe from South America (Kuijt & Lye 2005). In general, mistletoes draw sap from the host species using the transpiration stream (Fisher 1983). This is exaggerated by a high retention of cations in mistletoe tissue that increases the pressure gradient (Crates et al. 2022). Mistletoe-host relationships generally have a large xylem pressure potential gradient in favour of the mistletoe, though environmental conditions can reduce it to even (Scalon & Wright 2017). The host sap provides the source of water for the mistletoe and contains mobile organic and inorganic solutes including nutrients, organic nitrogen and nitrogen rich proteins, chelated ions, growth hormones, and enzymes (Fisher 1983; Scalon & Wright 2017). This can deny the host branch access to water and nutrients, resulting in the death of the limb beyond the haustorium (Watson 2019). This results in the same sap flow to the branch as before the infection while retuning none of the products of photosynthesis (Watson 2019).

The successful establishment rate of germinated seeds can vary wildly between mistletoe species and host species. Studies on *Arceuthobium* ‘dwarf mistletoes’ (Viscaceae family) have found successful establishment rates of up to 13% after 3.5 years (Smith 1977). However, other studies suggest the germination rates of *Arceuthobium* are much lower at 4.6% (Baker et al. 1981) to 5% (Carpenter et al. 1979). This low rate of successful germination appears to be mirrored in the limited studies into establishment of Loranthaceae mistletoes. Forestry and Timber Bureau (1968) found a 6%

establishment rate in a 3.5 year study on an *Amyema* mistletoe, suggested as likely to have been *Amyema miquelii* ‘Box Mistletoe’ by Lamont (1983). An ongoing reestablishment project by Watson (2022) in Melbourne, Australia has found an even lower rate of establishment for *Muellerina eucalyptoides* ‘Creeping Mistletoe’ seeded on *Platanus* ‘Plane Tree’. The reestablishment project inoculated 26 Plane Trees with 32 seeds per tree, resulting in the successful establishment of 24 of the 832 mistletoes after 1 year for an establishment rate of 2.87% (Watson 2022). 5 years into the reestablishment project a total of 5 individual mistletoes had reached maturity (flowering or fruiting) (Watson 2022). The project by Watson (2022) differs from the studies by Baker et al. (1981), Carpenter et al. (1979), the Forestry and Timber Bureau (1968) in two distinct ways that make it an unfit direct comparison. First, it does not account for the mortality of mistletoes dispersed to unsuitable substrates as the seeds were inoculated directly onto the host. Second, it is an establishment project of a mistletoe on an introduced, atypical host that *M. eucalyptoides* had not evolved to parasitise. The growth rates of Loranthaceae mistletoes vary greatly between species. Fast growing species, such as *Amyema preissii* ‘Wire Leaved Mistletoe’ have been observed to take as little as 9 months to reach maturity (flowering) when inoculated on *Acacia tetragonophylla* ‘Dead Finish’ (Watson 2019). However, other observations have shown that Loranthaceae mistletoes can be extremely slow growing. *Amyema quandang* ‘Grey Mistletoe’ has been observed to take in excess of two years before growing leaves when inoculated on *Acacia homalophylla* ‘Yarran’ (Watson 2019) and *M. eucalyptoides* has been observed taking up to one year to develop leaves when inoculate on *Platanus* trees (Watson 2022). These reported growth rates are informal observations as part of studies assessing other characteristics of mistletoes. The author Watson (2019) notes that there is a lack of formal studies into the growth rates of Australian mistletoes and provides only rough context to estimate age through the size of the mistletoe clump and the width of the host branch width.

In drought conditions, mistletoes often lose a significantly larger amount of water by surface area than the host (Crates et al. 2022; Fisher 1983). This is caused by a limited control of stomata, characteristic of the high transpiration rates used to maintain the pressure gradient over the host (Crates et al. 2022). Mistletoes also lack any form of water storage organ (Crates et al. 2022). This makes mistletoes sensitive to changes in moisture availability (Crates et al. 2022) and leads to a high mortality rate of mistletoes through evapotranspiration during extended drought conditions (Crates et al. 2022; Watson 2019). While persistent mistletoes can compromise the survival of the host through increased water stress during drought conditions, typically the mistletoe will perish before the host (Watson 2019).

2.1.2 Ecological Interactions of Mistletoes

Loranthaceae mistletoes have a network of interdependencies with their host plant, seed dispersers, pollinators, frugivores, and herbivores (Watson 2019; Watson & Herring 2012). They provide an important source of food for birds, insects and mammals (Anderson & Braby 2009; Braby 2006; Watson 2019; Watson & Herring 2012), as well as habitat and nesting sites (Barea 2008; Cooney

& Watson 2008; Cooney et al. 2006). They also have a complex relationship with the understory of forest ecosystems through a disproportionate rate of litterfall in drier climates (March & Watson 2007). This has led to modern literature highlighting their importance within forested ecosystems (March & Watson 2007; Stevens & Watson 2022; Watson 2022; Watson & Herring 2012). This represents a paradigm shift from the historical perspective on mistletoes that depicted them largely as unwelcome pests that reduce tree health (Gill 1961; Hawksworth 1983; Nicholson 1955). This paradigm shift is not mirrored unilaterally through the Australian research community with studies continuing to highlight the detrimental effects of mistletoe and methods to cull mistletoe populations (Carnegie et al. 2009; Jurskis et al. 2005; Kelly et al. 1997). This perspective is mirrored in many foreign studies into mistletoes, with a large volume of mistletoe papers focussed on the detrimental effects of *Arceuthobium* in North America (Oblinger & Andrea 2021; Ritter et al. 2017; Ritter et al. 2018)

Mistletoes rely on frugivorous birds for seed dispersal, with two groups: mistletoe specialists, and dietary generalists which include frugivores and opportunistic foragers (Watson 2013, 2019). There are two mistletoe specialist birds in Australia, *Grantiella picta* ‘Painted Honeyeater’ and *Dicaeum hirundinaceum* ‘Mistletoebird’ (Watson 2019; Watson & Herring 2012). These specialists have an exceptionally narrow dietary breadth for obligate frugivores (Rawsthorne et al. 2012) with a diet that consists of up to 90% mistletoe fruits (Reid 1989; Roxburgh 2007; Walsberg 1975). Both Australian mistletoe specialists have modified gastrointestinal tracts which allow the seed to pass the muscular gizzard without damage and allow the bird to defecate a viable seed (Watson 2019; Watson & Rawsthorne 2013). These mistletoe specialists have an important function in the dispersal of mistletoe seeds, however they preferentially visit sites with established mistletoe which leads to a contagious pattern that aggregates mistletoes on already infected hosts and hosts of the same species (Rawsthorne et al. 2012; Ward & Paton 2007). This limits the dispersal of mistletoe seeds at a landscape level through a positive feedback cycle that encourages mistletoe specialists to occupy areas with extensive mistletoe infections, providing access to habitat and food resources (Ward & Paton 2007). This results in restricted movement patterns that rarely result in the successful dispersion of a seed to an uninfected host (Rawsthorne et al. 2012; Ward & Paton 2007). This restricted distribution and movement of mistletoe specialists often leads to multiple mistletoe infections at the site of historic mistletoe specialist nests (Watson 2019).

Unlike mistletoe specialists, the non-selective movements of dietary generalists allow them to deposit seeds well beyond the boundaries of existing mistletoe infections (Rawsthorne et al. 2010; Watson 2019). Primarily frugivorous species known to regularly consume mistletoe and disperse viable seeds include: Spiny-cheeked Honeyeater, Singing Honeyeater, Grey Honeyeater, Olive-backed Oriole, Yellow-throated Miner, Fuscous Honeyeater, Red Wattlebird, and Silveryeye (Watson 2019). Additionally, a number of foragers opportunistically feed on mistletoes and may occasionally disperse viable seeds including: Rose-crowned Fruit-dove, Brown Cuckoo-dove, Black-faced Cuckoo-shrike,

Metallic Starling, and at least 12 other honeyeater species (Watson 2019). A study by Rawsthorne et al. (2010) found that *Acanthagenys rufogularis* ‘Spiny-cheeked Honeyeaters’ can deposit viable seeds up to 700m away from the mistletoe source based on flight patterns and a gut passage time of 40 minutes. Rawsthorne et al. (2010) suggests that during drought conditions the change in flight patterns would allow Spiny-cheeked Honeyeaters to distribute seeds up to 4km from the mistletoe source. Watson (2019) further suggests that external dispersal, where the mistletoe adheres to the bird, would allow for dispersal over greater distances than internal dispersal and allow for dispersal over unsuitable habitats such as the ocean. It is for this reason that Rawsthorne et al. (2010) and Watson (2019) suggest that dietary generalists play a larger role in establishment of distant mistletoe infections than mistletoe specialists. This suggests that dietary generalists may be more important for recolonisation after fire, but only if they make up a significant portion of the consumption of mistletoe fruits.

A large number of invertebrates have dependencies on mistletoes for food and habitat, but the extent of the research is limited (Watson 2019). A study by Anderson and Braby (2009) on *Decaisnina signata*, a tropical Loranthaceae mistletoe, found that 113 species of insects and spiders visited the mistletoe in an urban vegetation matrix. Anderson and Braby (2009) estimated the true species richness of this study to be 229 using incidence-based coverage estimators. This species diversity had no discernible association with the host tree species (Anderson & Braby 2009). This represents an exceptional invertebrate diversity, particularly in the families of Hymenoptera, Hemiptera, Araneae, and Lepidoptera (Anderson & Braby 2009). A study by Burns et al. (2011) found that insects inhabiting *A. miquelii* had the same diversity as their Eucalypt host tree at an order level but vary in individual species and abundance. A further study by Burns et al. (2015) confirmed that mistletoes and host trees support different species assemblages, with mistletoes showing a lower host-specific species diversity of insects and a high number of tourist insects. In addition, the litterfall of mistletoes has been observed to increase the species diversity and total biomass of arthropod communities beneath infected trees (Mellado et al. 2019); which additionally encourages proliferation of insectivores (Mellado et al. 2019)

Due to the pervasive communal interactions of mistletoes that modern literature has moved towards labelling mistletoes, in Australia and worldwide, as a keystone resource (March & Watson 2010; Watson 2017). Mistletoe as a keystone resource was first proposed by Watson (2001), on the foundations proposed by Terborgh (1986) into the importance of figs on the frugivorous communities that rely on them in neotropical forests, particularly during periods of scarcity. As a keystone species, it is proposed that mistletoes have a disproportionate impact on their communities, species distribution, and diversity (Sasal et al. 2021). The hypothesis by Watson (2001) relied on vertebrate species diversity, showing that species from 97 vertebrate families interact with mistletoes and species from 50 vertebrate families rely on them for nesting sites. Watson and Herring (2012) further supported the theory of mistletoes as a keystone resource through a study that showed the removal of Loranthaceae mistletoes from Eucalypt forests saw an average decline in avian species richness of 20.9%. The effect of mistletoe

removal was most apparent for woodland-dependent bird species declining by 26.5%, and woodland-dependent resident species declining by 34.8%. (Watson & Herring 2012). Watson and Herring (2012) further stipulate that the net loss from mistletoe removal may be higher than observed due to an increase in species diversity at control sites corresponding to changes in regional climate conditions. Watson (2017) notes that the mistletoe keystone hypothesis still requires a large amount of research, especially in the largely underrepresented tropical mistletoes. The mistletoe keystone hypothesis has been largely developed by Watson (2001; 2017); and Herring (2012) but is increasingly supported by the findings of other scholars (Napier et al. 2014; Těšitel et al. 2020).

2.1.3 Loranthaceae and Fire

The interactions between mistletoes and fire is a highly fragmentary field of knowledge with one notable exception, *Arceuthobium* dwarf-mistletoes, which have been highly researched in North America as they parasitise several commercial valuable coniferous species and are significantly detrimental to the health of the host plant (Shaw et al. 2004). Fire is considered the primary natural control agent for dwarf-mistletoes, so the increase in fire suppression practices is considered to have greatly contributed to the increase in distribution and abundance of dwarf-mistletoes (Shaw et al. 2004). Due to the different evolutionary history and biology, dwarf-mistletoes are not considered analogous to Loranthaceae mistletoes despite expressing some similarities with ecological interactions (Shaw et al. 2004). At the time of the comparison between *Amyema* (Loranthaceae) and *Arceuthobium* (Viscaceae) authored by Shaw et al. (2004) there was almost no literature on the interaction of Loranthaceae mistletoes and fire. However, since the release of this paper a limited number of studies in Western Australia have focussed on the effects of wildfire on mistletoes dynamics (Gosper & Prober 2020; Start 2011, 2013, 2015). Additionally, a paper by Kelly et al. (1997) assessing the manual application of fire as a treatment for mistletoes provides key insights into the processes of fire induced mistletoe mortality.

In a study assessing multiple control methods for *Amyema miquelii* ‘Box Mistletoe’ and *Amyema pendula* ‘Drooping Mistletoe’, Kelly et al. (1997) found that the mistletoes had subcortical buds for epicormic regrowth after defoliation, pruning or fire. However, the mortality rate from fire exposure was considerably higher than other control methods at 50% for *A. pendula* and 67% for *A. miquelii* after an average flame exposure of 47.3s (Kelly et al. 1997). Flame exposure resulted in canopy scorch and leaf death of all but 1 mistletoe, and no survivors had recovered their original canopy size within two years of the fire (Kelly et al. 1997). This suggests that the regrowth buds of the mistletoes are not sufficiently protected against fire (Kelly et al. 1997). Burned mistletoes recovered slower than pruned or defoliated mistletoes suggesting a more extensive physiological damage or different response (Kelly et al. 1997). In addition, larger mistletoes and higher mistletoes showed greater rates of survival than smaller or lower individuals (Kelly et al. 1997). Though the study did not assess wildfires, Kelly et al. (1997) extrapolates the results to predict that high severity fire would kill all, or almost all, mistletoes

in the crown; and low severity ground fires would be hot enough to scorch and kill low hanging canopy mistletoes. Kelly et al. (1997) also notes that 64°C is the temperature for instantaneous cell death for mistletoe tissue, which is reached for surface tissue within 10 seconds of the commencement of burning.

A study by Start (2011) categorised Australian Loranthaceae mistletoes into three groups based on the strategies utilised to persist in fire-prone environments, through survival adaptations or recolonisation:

1. *Resprouters*. Mistletoes capable of resprouting from the haustoral tissue after fire scorch. This included only two varieties of one species, *Amyema sanguinea* ‘Bloodwood Mistletoe’.
2. *Fire safe-host selectors*. Species highly specific to hosts which grow in fire protected environments such as rocky gorges, or in fire infrequent communities such as mangroves, riparian zones, or mulga woodlands.
3. *Rapid recolonisers*. Species with exceptionally low host specificity that can quickly recolonise burned areas.

A significant portion of the Loranthaceae species observed displayed no apparent fire-survival strategy, while a small number displayed more than one Start (2011). The strategies varied greatly depending on the environment with almost all species present in the arid Pilbara region displaying some form of fire-survival strategy (Start 2015), while very few species displaying some form of survival strategy in the mountainous Kimberley region (Start 2013). Common east coast species *A. bifurcata* and *A. miquelii* (Watson 2019) displayed no discernible fire-survival strategy (Start 2011). Species lack a fire-survival strategy are considered obligate seeders with no in-situ seed storage, and therefore must rely on dispersal to recolonise after fire events (Start 2011). While the studies by Start (2011, 2013, 2015) assess the impacts of long-term fire regimes on mistletoe population and distribution, they do not assess the recolonisation on a temporal or spatial scale. A study by Gosper and Prober (2020) into post-fire recolonisers assessed the effect of historic fires on the distribution of *A. miquelii* and *Lysiana casuarinae* ‘Casuarina Mistletoe’. It found that no recovery of post-fire colonisers had occurred in fire sites younger than 20 years. *A. miquelii* was present in intermediate fire sites (35-120 years), increasing in mature fire sites (140-200 years). The distributions were significantly reduced for intermediate and mature fire sights when compared to post-mature fire sites (>200 years). *L. casuarinae* had not recolonised any young, intermediate, or mature fire sites, only present in post-mature fire sites with excess of 200 years since the fire. These findings are supported by an ongoing, long term study referenced in Watson (2019) which has observed that mistletoes are still absent in a large number of high severity fire sites 20 years after the fire. However, as the study is ongoing the results and findings are not available to draw conclusions from. The study by Gosper and Prober (2020) theorises that mistletoes utilise the process of edge recruitment to recolonise after fires but does not address mechanics or recruitment rate. To date, no comprehensive study has assessed the processes by which mistletoes recolonise following high severity fire in a spatial or temporal scale.

2.2 Fire

Fires are a natural disruptive phenomenon that affects forests, grasslands, shrublands, and savannas globally (Giglio et al. 2013). Fire is a large-scale disturbance characterised by the consumption of complex organic molecules as fuel. Fires require four key conditions, also known as fire switches, to emerge. These fire switches are a) the presence of biomass or fuel, b) fuel must be dry enough to burn, c) the weather must be conducive for fire, and d) a source of ignition must occur (Bradstock 2010). Fires consume living and dead organic matter, including the products of plants considered inedible for herbivory, leaving waste consisting of simple organic, mineral, and gaseous biproducts in the form of carbon monoxide, carbon dioxide, and water (Bond & Keeley 2005). This makes fires an important biogeochemical process that interacts with the biosphere, geosphere and atmosphere (Bowman et al. 2012). Fire influences the climate through multiple interactions, including the release of heat, particulates, and gasses, and the effect on albedo through the removal of vegetation and scorching of surfaces (Bowman et al. 2012). The breakdown of complex organic molecules during fire acts to release important nutrients and recalcitrant carbon into the soil (Bond & Keeley 2005; Bowman et al. 2012), but can also increase susceptibility of the soil to erosion (Bowman et al. 2012). This differentiates it from other large-scale disturbances such as floods and cyclones, due to the interactions with numerous short-range and long-range feedbacks (Bowman et al. 2012). Additionally, it is differentiated as other disturbances are not characterised by the consumption of organic molecules (Bond & Keeley 2005; Bowman et al. 2012).

Fire regime is a term used to define the characteristics of a sequence of fire events within a discrete time frame and area (Collins 2012). The term fire regime arose from the need to generalise the highly variable characteristics and complex interactions that can dramatically change the behaviour and nature of fires in different regions or climates (Krebs et al. 2010). The terms usage became popular following a paradigm shift in the understanding of the ecological importance of wildfire on ecosystem health and maintenance, and follows a change in perception regarding fire suppression in the wake of several highly destructive wildfires in the United States during the 1950's and 1960's (Krebs et al. 2010). Since the terms early usage, the properties of fire regime have changed slightly. Early literature such as Gill (1975) define fire regime as the fire intensity, frequency, seasonality, and fire type within a discrete area. Modern literature often substitute fire intensity for a newer metric fire severity to resolve complications regarding the difficulty in measuring fire intensity, and predicting the biological impact of fire (Keeley 2009).

2.2.1 Fire Intensity and Severity

Fire intensity is the measure of the time-averaged energy flux of a fire, representing the thermal output created during the release of energy from the combustion of organic matter (Keeley 2009). It is a metric historically used for estimating the effect of a fire on buildings and predicting the effectiveness

of fire suppression. This was commonly adapted into fireline intensity for wildfires, an alternative measurement which represents the rate of heat transfer along a fire front to inform forestry management and fire suppression practices (Byram 1959). However, the effect of similar fire intensities can vary greatly between vegetation communities and regions, new metrics were necessary to inform ecological management.

Fire severity is the measure of the ecological impact of an individual fire on the affected ecosystem (Gordon, Price & Tasker 2017; Keeley 2009). Fire severity generally represents the portion of vegetation consumed but does not necessarily relate to one definable metric, varying in its application between ecosystems (Keeley 2009). A number of metrics have been proposed to define fire severity including: tree mortality (Keeley 2009), degree of biomass change through foliage loss or the diameter of remaining terminal branches (Dickinson & Johnson 2001; Moreno & Oechel 1989; Tolhurst 1995), changes to soil characteristics (Neary et al. 1999; Wells et al. 1979), and changes to visible spectrum via remote sensing (Chafer et al. 2004; Gordon, Price & Tasker 2017; Veraverbeke et al. 2011). For Eucalypt dominated sclerophyll forests in Australia, it is common for fire severity to be determined from the degree of consumption of biomass in a vertical direction (e.g. Etchells et al. 2020; Palmer et al. 2018). However, it is often more practical to use remote based sensing techniques (e.g. Barker et al. 2022; Chafer et al. 2004; Denham et al. 2016; Gordon, Price & Tasker 2017). This facilitates the creation of a fire severity analysis across the entire fire affected area and can be validated through field sampling.

To determine fire severity using remote sensing several indices have been proposed, comparing the difference between pre- and post-fire images (Gibson et al. 2020). They are typically divided into reflectance based models and fractional cover models (Gibson et al. 2020). Reflectance based models compare the change in reflected light bands between the pre- and post-fire images and often represent the degree of loss of photosynthetic biomass (Chafer et al. 2004; Gibson et al. 2020). Fractional cover models determine the change in area of discrete categories, often categorised into photosynthetic and non-photosynthetic surfaces based on reflectance bands (Gibson et al. 2020). This compares the difference between plant cover and bare ground. Examples of remote sensing indices for fire severity include: differenced normalised burn ratio (dNBR); relativised dNBR (RdNBR); relativised change in total fractional cover (RdFCT); and change in bare fractional cover (dFCB), the differenced normalised differenced vegetation index (dNDVI) and the differenced Bare Soil Index (dBSI) (Gibson et al. 2020). Gibson et al. (2020) compared the accuracy of remote sensing techniques to field validation, finding that the models listed above have a mean accuracy of 88% across all classes of fire severity when using Sentinel 2 imagery. Mean classification accuracy was highest (>85%) for results in unburnt regions and severities of high and greater, while most models saw a significant drop in accuracy (70-80%) for low to middle severity classes (Gibson et al. 2020). Gibson et al. (2020) also found that model accuracy was highest in composite models that incorporate both a reflectance and fractional cover model.

When referring to fire severity within forest structures, many studies use a classification system based on the degree of vegetation change. Table 1. as presented by Keeley (2009) is an example of a characterisation system for determining fire severity through field observation. However, with remote sensing there is a need for more specific values for the categorisation of fire severity. Table 2. modified from Gibson et al. (2020) provides interpretation cues for remote sensing based technology, to determine the fire severity and expected effect on photosynthetic biomass.

Table 1. The matrix originally proposed by Ryan and Noste (1985) that related changes in aboveground vegetation and soil organic matter to fire severity has generally been simplified to a table such as that below; modified from Ryan (2002) and Turner et al. (1994), as presented by Keeley (2009)

Fire Severity	Description
Unburned	Plant parts green and unaltered, no direct effect from heat
Scorched	Unburned but plants exhibit leaf loss from radiated heat
Light	Canopy trees with green needles although stems scorched. Surface litter, mosses, and herbs charred or consumed. Soil organic layer largely intact and charring limited to a few mm depth
Moderate or severe surface burn	Trees with some canopy cover killed, but needles not consumed. All understorey plants charred or consumed. Fine dead twigs on soil surface consumed and logs charred. Pre-fire soil organic layer largely consumed
Deep burning or crown fire	Canopy trees killed and needles consumed. Surface litter of all sizes and soil organic layer largely consumed. White ash deposition and charred organic matter to several cm depth

Table 2. Aerial photo interpretation classification of fire severity, adapted from (Hudak et al. 2004), (McCarthy et al. 2017), (Collins et al. 2018) and Gibson et al. (2020)

Fire Severity	Description	Interpretation Cues (False colour infra-red aerial photos)	% Foliage Fire Affected
Unburnt	Unburnt surface with green canopy	Dark red (live understorey) between the dark red tree crowns	0% canopy and understory burnt
Low	Burnt surface with unburnt canopy	Dark grey (burnt understorey) between the dark red tree crowns	> 10% burnt understory
Moderate	Partial canopy scorch	A mixture of green, orange, and brown colours in tree canopies	20–90% canopy scorch
High	Full canopy scorch (\pm partial canopy consumption)	No green or orange, but an even brown colour in tree canopies	> 90% canopy scorched < 50% canopy biomass consumed
Extreme	Full canopy consumption	Mostly black and dark grey, largely no canopy cover	> 50% canopy biomass consumed

2.2.2 Fire Behaviour

The behaviour of fires is determined through numerous factors including: fuel moisture content, fuel abundance, distribution of fuel stratum, wind, and topography (Sullivan et al. 2012). Fuel moisture determines the combustion characteristics, resultant fire behaviour, and the energy required to combust fuel (Sullivan et al. 2012). Fuel moisture content can vary greatly with climate, atmospheric conditions (Sullivan et al. 2012), water availability, and plant drought adaptation (Yebra et al. 2013). Topography

and slope play an important role in the propagation of fire (McArthur 1967; Sullivan et al. 2012) and the behaviour of spotfires (Storey et al. 2021). The relationship between slope and fire is not entirely clear, contested between linearly additive (e.g. Viegas 2004; Wagner 1988) and complex relationships (e.g. Wu et al. 2000). Wind predominantly determines the rate of spread through modifying the radiative preheating of fuel (Butler et al. 2004), modifying the degree of fuel bed fire immersion (Beer 1995), and determining the distribution of spot fires from airborne burning material (Storey 2021; Storey et al. 2021). The rate of spread of the fire is not directly tied to wind or topography and can vary dependent on fuel properties (Sullivan et al. 2012).

For wildfires, fuel is any living or dead vegetation that will readily burn (Sullivan et al. 2012). Fires are often characterised based on the predominant fuel type as fuel type and availability can vary greatly between environments (Sullivan et al. 2012). The fuel structure of an environment is important in determining the fire characteristics for risk management (Barker et al. 2022) Australian Eucalypt forests have a complex fuel structure comprised of multiple strata that affect the fire characteristics (Sullivan et al. 2012). Sullivan et al. (2012) defines the fuel strata in Australian forests based on the characteristic of the fire they contribute to: flame height, flame depth behind fire front, smouldering period, indirectly flammable, non-flammable material. Typical fuel types are summarised in Table 3.

Table 3. The fuel strata, associated strata composition, and fire characteristic that they contribute to for a typical Australian forest dominated by Eucalypts. Adapted from Sullivan et al. (2012)

Fuel Strata	Typical Strata Composition	Fire Characteristic
Low density fuels	Small fast burning fuels. Primarily the loosely compacted layer of leaf litter, twigs, and low shrubs on and near the forest floor	Flame height
Mid density fuels	Small, slow burning fuels. Primarily the upper part of the leaf litter layer and larger twig components from 6mm to 25mm embedded within it	Flame depth behind fire front
High density fuels	Dense and larger fuels. The duff (lower compacted part of the leaf litter layer), dead fuels larger than 25mm, and decorticated bark of stringybark type trees.	Smouldering period
Indirectly flammable	Fuels that can only burn when supported by the combustion of other fuels. Sparse, high, dead fuels and living fuels (such as the canopy)	-
Non-flammable	Fuels that do not burn during a fire due to their location, moisture content, or size. Often live trunks and moist logs.	-

Forest fuels are also characterised by their vertical distribution. This categorises them into regions of bulk density that can suggest fire behaviour (Sullivan et al. 2012). Surface fuels typically contain horizontally layered, small fallen biomass including leaves, bark, and twigs (Sullivan et al. 2012). Near-surface fuels typically contain low growing biomass with no discernible orientation including grasses, low shrubs, creepers, and collapsed taller shrubs, but can also contain suspended dead biomass sourced from overstory trees (Sullivan et al. 2012). Elevated fuels generally contain oriented vertically larger shrubs, young trees, and the epicormic regrowth of overstory species (Sullivan et al. 2012). The

overstory is the final category of fuel and is populated by the crowns of larger trees (Sullivan et al. 2012). The surface and near-surface fuel layers provide the most biomass and energy by weight for the fire, while the elevated and overstory fuel layer are the most important for determining the maximum height of the fire (Sullivan et al. 2012). In addition, bark sourced from trees typically associated with the overstory are easily lofted while burning and can generate spotfires downwind of the fire front (Sullivan et al. 2012). This suggests that the characteristics of the surface and near-surface fuel layers are more important for determining the fire intensity, while the characteristics of the elevated and overstory fuel layers are more important for determining the fire severity. This suggests that the characteristics of the elevated and overstory fuel layers will contribute to the rate of mistletoe survival during a fire.

2.2.3 Australian Bushfire

Annually, Australia accounts for an average of 13% of the global mean fire area (Giglio et al. 2013) despite comprising only 5% of the global terrestrial area (Geoscience Australia 2004). The prevalence of fire in Australia is a characteristic of the continent's geographic location and subsequent climate. southern Australia is largely situated in the sub-tropics between 20° S and 35° S, characterised by high pressure systems, and dry, clear weather (Lindesay 2003). The position of southern Australia creates a climate where the north, east, south-east and south-west coasts are relatively wet with rainfall originating from tropical and midlatitude disturbances, while the interior and west coast are dry (Lindesay 2003). The low precipitation of the interior is exaggerated by continent scale climatic phenomena that can decrease rainfall. The El Niño Southern Oscillation (ENSO) is a large scale ocean and atmospheric process that causes variation in Australian rainfall, streamflow, and drought conditions (Chiew et al. 1998). The variation caused by the ENSO causes multi-year periods known as El Niño events, associated with dryer than average conditions and high temperatures across the eastern half of the continent (Lindesay 2003). This facilitates the drying of fuel for extended periods of the year and promotes severe fire conditions (Sullivan et al. 2012). Likewise, the shorter La Niña events of higher precipitation that promotes the abundant rapid growth of short lived vegetation that elevates fire risk for subsequent years (Sullivan et al. 2012). Additional climate phenomena such as the Pacific Decadal Oscillation further exaggerate this by acting as underlying signals that amplify or mediate the effects of the ENSO events (Lindesay 2003; Verdon et al. 2004). The low rainfall conditions in the sub-tropics have produced a regime of widespread fire in Australia, which is amplified during periods of drought caused by events like El Niño. South-eastern Australia has a climate characterized by hot, dry summers and cold, wet winters (Lucas et al. 2007). This allows for fuel growth during the wet winter and spring before the fire risk increases during the dry summers (Lucas et al. 2007).

The dominance of fire on the Australian continent is not a new regime, having dictated the evolution of the continent for millions of years (Deb et al. 2020). Modern fire-adapted sclerophyllous lineages like

Proteaceae and Myrtaceae begin to appear in the Gondwanan fossil records between the middle Cretaceous to middle Eocene (Lamont & He 2012; Mack & Milne 2015), a period where the continent was dominated by wet temperate forest (Rundel et al. 2016). The separation of Australia from the Antarctic Gondwanan Relic in 33-30 Ma resulted in the slow aridification of Australia, a sharp reduction in wet temperate forest, and the radiation of sclerophyll forest and shrubland (Hopper & Gioia 2004; Rundel et al. 2016). During the Pleistocene and into the Holocene fires had become common across all ecosystems, forcing the retreat of wet forests into isolated rainforest sanctuaries and allowing further diversification of sclerophyll forest (Pyne 2017). A composite paleo-fire record by Mooney et al. (2012) has addressed the evolution of fire regimes in Australia dating to 70 ka, showing a highly variable fire regime over millennium scales. The model displays no discernible lag between climatic changes and resulting changes to biomass burned (Mooney et al. 2012). This suggests a strong response in fire regime to temperature changes from climatic variability (Mooney et al. 2012). Models have shown a large increase in biomass burned around 50 ka, synchronous with the arrival and radiation of *Homo sapiens* (Lynch et al. 2007; Mooney et al. 2012). The effect early humans had on the fire regime of Australia is a contentious field of study. Some literature has linked the increase in biomass burned to the introduction of practices like firestick farming and cultural burning, the resulting trophic cascade caused by the overhunting and extinction of herbivorous megafauna (Johnson 2016; Miller et al. 1999), or the collapse of the Holocene monsoon due to insolation changes from cultural burning (Miller et al. 2005). Other literature rejects this hypothesis as they do not account for large scale climate variation events like the Dansgaard–Oeschger event of 49.28 ka which may better explain the changes to biomass burned (Lynch et al. 2007; Mooney et al. 2011). The period between the 50 ka and 1800 CE is characterised by a relatively stable fire regime before sharply increasing between 1800 and 1900 CE (Mooney et al. 2012). The period between 1800 and 1900 CE accounts for the largest increase in biomass record regardless of temporal window (Mooney et al. 2012). Mooney et al. (2012) attributes this to the impact of European settlement and the propagation of agriculture. The model then shows a significant decrease in biomass burned following 1900 CE attributed to the implementation of fire suppression and forest fragmentation, however the biomass consumed by fires is still above the pre-1800 CE baseline (Mooney et al. 2012).

The historic fire regime of Australia has played an important role in the evolution of flora and fauna on the continent for millions of years (Deb et al. 2020). In Eastern Australia, many plants are highly adapted to persist through fire events (Barker et al. 2022). Post-fire responses of plants are divided into two broad categories, reseeding plants and resprouting plants (Barker et al. 2022; Burrows 2013). Reseeding plants, or obligate seeder species, are usually killed during a fire event and recover their population through seedbanks stored underground or in the canopy (Barker et al. 2022; Gill 1981). Resprouting plants often survive fire events and re-establish through above-ground epicormic buds (Burrows 2013; Clarke, PJ et al. 2013), below ground lignotubers (Burrows 2013; Clarke, PJ et al.

2013), or in rarer cases apical resprouts (Burrows 2013). Additional categories have been added to the existing post-fire response framework to include pyrophobic communities, including post-fire colonisers and fire vulnerable species (Gosper & Prober 2020; Prior & Bowman 2020). Post-fire colonisers are species that rely on dispersal to recolonise high severity burn areas due to an inability to resprout or reseed following high severity fire (Prior & Bowman 2020). Fire vulnerable species encompasses all species that cannot readily recolonise and are unable to resprout or reseed following high severity fire (Prior & Bowman 2020). Eucalypt type forests dominate Australian forests accounting for 75.4% of Australia's forested area as of 2018 (Downham & Gavran 2019). Eucalypts, including the genera's *Angophora*, *Corymbia*, and *Eucalyptus* (Burrows 2013), show a wide variety of survival strategies including lignotuber sprouting, combination (lignotuber and epicormic) resprouting, epicormic resprouting, and some species only displaying obligate seeding (Nicolle 2006). Acacia type forest accounts for an addition 8.1% of Australia's forested area (Downham & Gavran 2019). *Acacia* have long-lived soil seedbanks that germinate in response to fire (Gordon, Price & Tasker 2017). In areas with infrequent fire *Acacia* persist in a dormant state as viable seeds in the soil seedbank rather than adult shrubs (Gordon, Price & Tasker 2017).

In Australia, many floral communities are also highly adapted to increase the flammability of the environment, with a strong interdependency with fire (Bowman et al. 2012). The theory that flora evolved pyrophytic characteristics that increase the risk of fire is prevalent in older literature, popularised by the Mutch hypothesis (Bowman et al. 2012; Mutch 1970). This theory is founded on the idea that fire as an environmental pressure has selected characteristics of plants that enhance the flammability of the plant community (Mutch 1970). The Australian Eucalypt is used by Mutch (1970) as an example of an inherited flammability trait to fortify this hypothesis as they grow thin, dry leaves, containing up to 3% eucalyptus oil by weight that burn readily. However, recent literature disputes this theory, suggesting that flammable characteristics did not evolve to promote flammability. Suggesting that pyrophytic traits developed through the process of exaptation, by which flammable traits arise in response to other selective pressures like herbivory, drought, and low soil fertility (Bowman et al. 2012; Bradshaw et al. 2011). Schwilk and Kerr (2002) propose an additional theory suggesting that flammable traits become widespread through genetic niche-hiking, where flammable traits increase without direct selective advantage. This process works when traits are found on alleles with characteristics that do provide a selective advantage, which allows the flammability trait to indirectly propagate. Schwilk and Kerr (2002) use this to explain the invasion of traits into spatial populations without direct advantage.

Anthropogenic climate change has the potential to change fire regimes through interactions with three of four fire switches, directly affecting fire weather and fuel conditions, while indirectly affecting fuel load and structure (McColl-Gausden et al. 2022). The frequency and magnitude of fire weather has been increasing in Australia since the 1960's, with the largest proportional increases seen in south-eastern Australia with the frequency of fire weather days increasing by 49% between 1973 to 2010 (Clarke, H

et al. 2013). The increase in fire weather mirrors increasing temperature trends in Australia since the 1960's, associated with climate change (Clarke, H et al. 2013). Increasing climate temperatures also affect the moisture deficit which has significant impacts on the drying of fuels (Caccamo et al. 2012). A global increase has been observed in the drying of and total amount of flammable fuels in wildland ecosystems (Ellis et al. 2022). Changes to the moisture deficit of fuel has two-fold effect, increasing the amount of flammable fuels, and increasing the connectivity of flammable fuels (Caccamo et al. 2012). These changes to fire weather and fire climate interact with biotic feedbacks that can influence the accumulation of fuel and the structure of fuel which affect fire regimes (McColl-Gausden et al. 2022). Bradstock (2010) notes that the elevation of atmospheric CO₂ levels can limit plant growth and biomass production, however postulates that this is less critical in Australian Eucalypt forests which are likely to see increases in fire severity, burned area, and the compounding effects of drought.

2.3 The Warrumbungle National Park

The Warrumbungle National Park [WNP] (-31.286405368460617, 148.99704162536239) is located within central-northern New South Wales, Australia. It is 33km west of the nearby town of Coonabarabran and 335km northwest of Sydney (NPWS 2012). The WNP is administered by the National Parks and Wildlife Service Coonabarabran Area Office and is accessible by John Renshaw Parkway, a sealed road that travels east-west through the park, roughly bisecting it into a northern and southern region. The WNP consists of 23312 hectares of land reserved under the *National Parks and Wildlife Act (NSW)(1974)* (NPWS 2012). The park is situated in the remote, rugged Warrumbungle Range of the upper Castlereagh River Catchment, but does not encompass the entire Warrumbungle Range (NPWS 2012). The National Park has been protected since 1936 as the Warrumbungle National Monument with the intent of preserving the unique geological and scenic features, but was not established as a National Park until the 1953 purchase of 3360 hectares of the Mountain Range (NPWS 2012). Land re-establishments and buybacks from the surrounding rural properties has added to the park to increase it to its current size.

The Warrumbungle Range is renowned for its particularly unique geological features, including large spires, dykes, cliffs, and bluffs that surround a large central valley. The Warrumbungle Range and the geological features are the remnants of an extinct Miocene age shield volcano that erupted through the Jurassic-Permian sedimentary basin (Bull et al. 2020). Extensive vulcanism associated with the gradual and continuous differentiation of magma at crustal depths extruded through the central vent, but also intruded through a series of side vents and fractures in the central dome leading to the formation of the dykes, sills, and domes associated with the National Park (Bull et al. 2020). The post-volcanism history of the central vent was associated with a series of on-and-off migrations of magmatic activity that lead to the circulation of iron- and sulphur-rich fluids and the development of oxidised and pyritic rocks (Bull et al. 2020). This lead to the excessive weathering of the central vent and the formation of the

central valley (Bull et al. 2020). This heavily mountainous region supports a mixture ecological communities reliant on sandstone, acid volcanic, and igneous substrates (Hunter 2008a).

The WNP is largely situated in the Brigalow Belt South bioregion and borders the Darling Riverine Plain bioregion and contains a diverse habitat range (NPWS 2012). The WNP conserves large intact areas of common ecological communities as well as sections of uncommon ecological communities (Hunter 2008a) As of 2008, the park had 779 known vascular plant species representing 397 families and 111 genera (Hunter 2008a; NPWS 2012). The park contains 11 native plant species of conservation concern including 10 listed ‘Rare or Threatened Australian Plants’ and 1 species listed as vulnerable by the *Environmental Protection and Biodiversity Conservation Act (Cth)*(1999) (Hunter 2008a). No threatened or vulnerable species in the WNP are Loranthaceae or Viscaceae. The park has been heavily disturbed by historic agricultural activity which presents a large threat to the park through weeds (Hunter 2008a). The parks vegetation is divided into 9 distinct ecological communities, summarised in Table 4. This includes the vulnerable ‘White Box - Yellow Box - Blakely’s Red Gum Grassy Woodland’ ecological community (Hunter 2008a). The WNP represents the highest diversity of vegetation species of any reserve on the North Western Slopes with a high beta diversity and species richness between individual test sites (Hunter 2008a). This is attributed to the incorporation of a diverse topographic environments within the reserve created by the Warrumbungle Range (Hunter 2008a). (Hunter 2008a)

Table 4. Floristic communities and their reservation status as presented by (Hunter 2008a) and used in the Warrumbungle Plan of Management (NPWS 2012)

Floristic Community	Reservation Status
C1: Red Stringybark – Apple	May only be known from Mt Kaputar, the Liverpool Range and the Warrumbungle’s. Should be considered rare in distribution and vulnerable to disturbances and climate change but adequately reserved locally.
C2: Black Pine – Ironbark	Well reserved locally and across its range. Not of concern.
C3: White Box – Ironbark – White Pine	Well reserved locally and across its range. Not of concern.
C4: Apple – Yellow Box – Red Gum	Parts of this community fall within the Grassy Box – Gum Woodlands endangered ecological community determination of the TSC & EPB&C Act.
C5: Patterson’s Curse – Weeping Grass	Highly disturbed, not of conservation significance.
C6: Speargrass grassland	Highly disturbed, predominantly not of conservation significance. *Some areas are intact Grassy Box – Gum Woodland and are thus endangered ecological communities.
C7: Ironbark – Bloodwood – Scribbly Gum	Well reserved locally. Not of concern.
C8: Motherumbah – White Pine	Only known from disjunct localities in Mt Kaputar NP and the Warrumbungle’s. Should be considered adequately reserved but rare.
C9: Motherumbah – Bloodwood	Disjunct and of limited extent but much more widespread than Community 8. Should be considered adequately reserved but rare in the landscape.

2.3.1 Mistletoes of the Warrumbungle National Park

There have been no comprehensive studies into the distribution of mistletoes within the WNP. Two general vegetation surveys provide insight into the previously recorded mistletoes within the WNP. The vegetation survey by Hunter (2008a) contains a list of known mistletoes within the park, however some species listed have outdated taxonomic names. BioNet Atlas is a database maintained by the NSW Department of Planning and Environment et al. (2022) that contains a list of reported mistletoe species in the park that have been verified and listed. The BioNet Atlas report contains identification reports listed for the park between October 1899 and December 2007. The two survey both list the same species present within the park. The BioNet Atlas used updated scientific names and was verified against (Watson 2019). The surveys have been collated in Table 5. The WNP's location in central-northern NSW and lack of comprehensive mistletoe vegetation survey suggests that a greater mistletoe abundance than observed may be possible. Many species of mistletoes have highly restricted host or ecological complex preferences (Start 2011, 2013, 2015) that suggest they may be present in isolated communities of small abundance through the WNP.

Table 5. Previously recorded mistletoes within the WNP. Records sourced from Hunter (2008a) and BioNet Atlas, NSW Department of Planning and Environment et al. (2022). Associated host information modified from Watson (2019).

Family	Scientific Name	Common Name	Associated Hosts
Loranthaceae	<i>Amyema bifurcata</i>	Forked Mistletoe	Generally <i>Eucalyptus</i> , occasionally <i>Angophora</i>
	<i>Amyema cambagei</i>	Needle-leaf Mistletoe	<i>Casuarina</i> and <i>Allocasuarina</i>
	<i>Amyema linophylla</i>	Buloke Mistletoe	<i>Casuarina</i> and <i>Allocasuarina</i>
	<i>Amyema miquelii</i>	Box Mistletoe	Generally Eucalypt and some <i>Acacia</i>
	<i>Amyema pendula</i>	Drooping Mistletoe	Relatively few species of Eucalypt and some <i>Acacia</i>
	<i>Amyema quandang</i>	Grey Mistletoe	Obligate <i>Acacia</i> parasite
	<i>Dendrophthoe glabrescens</i>	Smooth Mistletoe	<i>Acacia</i> , Eucalypt, <i>Melaleuca</i> , and <i>Tristania</i>
	<i>Lysiana exocarpi</i>	Harlequin Mistletoe	<i>Acacia</i> , <i>Casuarina</i> , <i>Allocasuarina</i> , <i>Cassia</i> , <i>Eremophila</i> and <i>Santalum</i>
	<i>Muellerina bidwillii</i>	Callitris Mistletoe	Obligate <i>Callitris</i> parasite
Viscaceae	<i>Muellerina eucalyptoides</i>	Creeping Mistletoe	Most closely associated with Eucalypt, but can colonise exotic trees
	<i>Notothixos cornifolius</i>	Kurrajong Mistletoe	Most closely associated with <i>Brachychiton</i> species and other Malvaceae family hosts.

BioNet Atlas Loranthaceae results generated with search queries. 1. Species or Group: Loranthaceae Family, 2. Legal Status: All Records, 3. Area Selected: Warrumbungle NP, 4. Period of Results: All Records, 5. Status: Valid Records Only. Report was generated on March 17, 2022.

BioNet Atlas Viscaceae results generated with search queries. 1. Species or Group: Viscaceae Family, 2. Legal Status: All Records, 3. Area Selected: Warrumbungle NP, 4. Period of Results: All Records, 5. Status: Valid Records Only. Report was generated on October 21, 2022.

2.3.2 The 2013 Wambelong Fire

Prior to the start of the Wambelong fire, the WNP had previously been evacuated on the 8th of January 2013 due to a period of extreme to catastrophic fire conditions, but the park was reopened in the following days. The Wambelong Fire was first reported on the 12th of January 2013, when smoke was reported at 4:00pm a short distance west of the Wambelong camping area (Brown et al. 2015; Murphy 2013). The weather conditions were conducive for fire weather with extremely high temperatures of 42.9°C, low humidity of 19%, and mild windspeeds of 13.3 km/h. The fire is estimated to have burned 25 ha by the end of the day but was declared contained by the RFS (Murphy 2013). On the 13th a backburning operation was commenced and subsequently abandoned as fire conditions worsened and catastrophic windspeeds began to pick up allowing the fire to cross the firebreak of John Renshaw Parkway. Section 44, used to defines fires that are unlikely to be controlled, was declared at on the 13th which placed moved the management authority of the fire from NPWS to RFS. At 3:57pm on the 13th the fire was declared out of control and an Emergency Warning 5 with an Evacuation Order was put in place for all citizens between the WNP and 5km west of Coonabarabran (Brown et al. 2015). On the 28th of January the section 44 of the fire was revoked returning management authority to the NPWS, and the fire was officially declared extinct on the 21st of February after burning for 41 days (Brown et al. 2015).

During this time the fire burned 55000 ha of land, destroying 53 homes and 131 other buildings, and killing 847 sheep and 318 cattle (Murphy 2013). The fire burned between 90% (Gordon, Price & Tasker 2017; Gordon, Price, Tasker, et al. 2017) to 95% (Brown et al. 2015; Murphy 2013; Tulau et al. 2019) of the WNP, with 72% of that area at high or extreme severity (Tulau et al. 2019; Yang et al. 2018). The areas of higher severity are characterised by total crown consumption of the forest, with low severity areas acting as refugia for biota (Gordon, Price & Tasker 2017). This had been the first fire in the WNP of such severity in over 60 years (Gordon, Price, Tasker, et al. 2017). The fire in the park was followed by an event of over 100mm of rain between the 18th and 23rd of January, followed by a severe storm on February 1st that brought between 57mm and 90mm of rain to the park, 80% within an 18 minute period (Tulau et al. 2019; Yang et al. 2018). This caused a mass erosion event including debris flow and flash flooding (Tulau et al. 2019). Following the fire the vegetation has been characterised by extensive but patchy regrowth that can vary greatly with severity and environmental history (Gordon, Price & Tasker 2017). Following the high severity fire significant alterations to the forest structure and distribution of ecological communities has also been noted, with large increase in *Acacia* abundance and a decrease in *Callitris* abundance (Denham et al. 2016; Gordon, Price, Tasker, et al. 2017). A fire free period in excess of 30 years may be required or fire vulnerable communities such as *Callitris* may risk extirpation (Denham et al. 2016) with significant implications for long term management and biodiversity.

Chapter 3. Research Design:

The Warrumbungle National Park has been chosen to assess the degree in which a fire vulnerable obligate coloniser is impacted by high severity fire, and the processes in which they use to re-establish to persist at a landscape level in a regime of frequent fires. Mistletoes are an ideal candidate for the study as an obligate coloniser that produces no long-term seed bank and cannot resprout after significant canopy scorch. Additionally, mistletoes align with the interests of the Department of Planning and Environment due to their importance to avian biodiversity and the critically endangered Regent Honeyeater. The WNP provides an ideal location for this thesis as it was affected by a high-severity megafire just under a decade ago. This fire should provide insights into the effect of high-severity fire on obligate colonisers, which will become increasingly important as fire frequency and severity increases with climate change.

3.1 Field Methodology

The survey was conducted entirely within the boundary of the WNP. Survey sampling was conducted across 82 transects gathered over two sampling periods. The first period was conducted from the 30th of March to the 31st of March 2022 and will be referred to as the preliminary period (PLM). The second period was conducted from the 26th of June to the 9th of July 2022 and will be referred to as the main period (MAIN). Some results from the preliminary period have been excluded from the data analysis as they followed different methodology to the main trip and may have caused issues with the data interpretation. The external data sources used in this thesis have been outlined in table 6.

Table 6. The data types, source, format, and resolution (where applicable) used for this thesis

Data	Source	Format	Resolution
Wambelong Fire rDNDVI Fire Severity Map	NSW Department of Planning and Environment (<i>unpublished data</i>)	Raster	5m
Warrumbungle NP Vegetation Map	Hunter (2008b)	Polygon	-
Warrumbungle NP Loranthaceae Survey	NSW Department of Planning and Environment et al. (2022)	Table	-

3.1.1 Fire Severity

The Wambelong fire severity map (Figure. 2.a.) used for this thesis was provided by the Department of Planning and Environment and is currently unpublished data. The severity map was calculated through relative Delta Normalized Differentiated Vegetation Index (rDNDVI) of satellite photos by RapidEye Imagery. The Normalized Differentiated Vegetation Index (NDVI) is a property calculated from the near-infrared and red colour band reflectance values of a vegetated surface (Chaker et al. 2004; Veraverbeke et al. 2011). NDVI is calculated by the formula $(p_{NIR} - p_{red}) / (p_{NIR} + p_{red})$ where p_{NIR} is the near-infrared light band and p_{red} is the red-light band. NDVI represents the amount of

photosynthetic vegetation in each pixel and is used to quantify the vegetative health of terrestrial ecosystems (Chafer et al. 2004). The rDNDVI compares the pre and post fire NDVI and the relative difference between the values to determine the percentage of photosynthetic biomass consumed by the fire. This data has a resolution of 5 meters and has been validated by the DPE through field observations.

The fire severity is divided into 4 categories: unburnt, low, moderate, and high. The unburnt severity encompasses all parts of the park with vegetation that were unaffected by the fire. Low severity is areas of the fire that had an understory burn with a small degree or no crown scorch. Moderate severity includes areas with an understory burn that had a high degree of crown scorch. High severity encompasses regions of the park where the crown burned or was consumed. Areas of the park that were unable to be verified by the rDNDVI analysis, including rocks, cliffs, roads, and cleared land, were categorized as unclassified. Mistletoes located within the unclassified layer were compared to their host fire health rating to determine the local fire severity, outlined in table 8. When determining the mean and median severity of each transect the unclassified severity was excluded from all calculations.

3.1.2 Ecological Communities

The ecological community map (Figure 2.b.) used for this thesis was developed by Hunter (2008b) on behalf of the NPWS Narrabri Region. The ecological communities used in the dataset are outlined in table 5. The ecological communities were determined by 20 x 20 m survey sites that describe the dominant species and structural characteristics the area. The ecological community map was created through a combination of techniques including ground-truthing, landscape analysis, and stereo interpolation of 1:50000 aerial photos. Accuracy of the dataset is unknown with some anomalies having been confirmed by National Parks & Wildlife Service (Hunter 2008b).

3.1.3 Transect Sampling

Mistletoes were sampled along transects selected to provide a balanced sample across the range of fire severities. Transects lengths ranged from 233 meters to 773 meters, with an average length of 543 meters. While each transect has one dominant fire severity class, many transects traversed more than one fire severity class. The large unburnt regions of the park were determined unfit for sampling allowing only small isolated unburnt regions to be sampled. The large unburnt region along the Tara access trail was dominated by Speargrass grassland, and the large unburnt region along Gunneemooroo contained large sections of cleared land around small copse of suitable host trees. 5 transects were chosen for the central valley region of the park. The region was formally cleared land but has been subject to revegetation programs (NPWS 2012). Transects within the central valley follow the revegetation stands and do not cover the sections of cleared grassland dominated by *Echium plantagenium* ‘Patterson’s Curse’, *Microlaena stipoides* ‘Weeping Grass’, and *Verbena bonariensis* ‘Purple-top Vervain’ which lacked any suitable mistletoe host species. The central valley showed signs

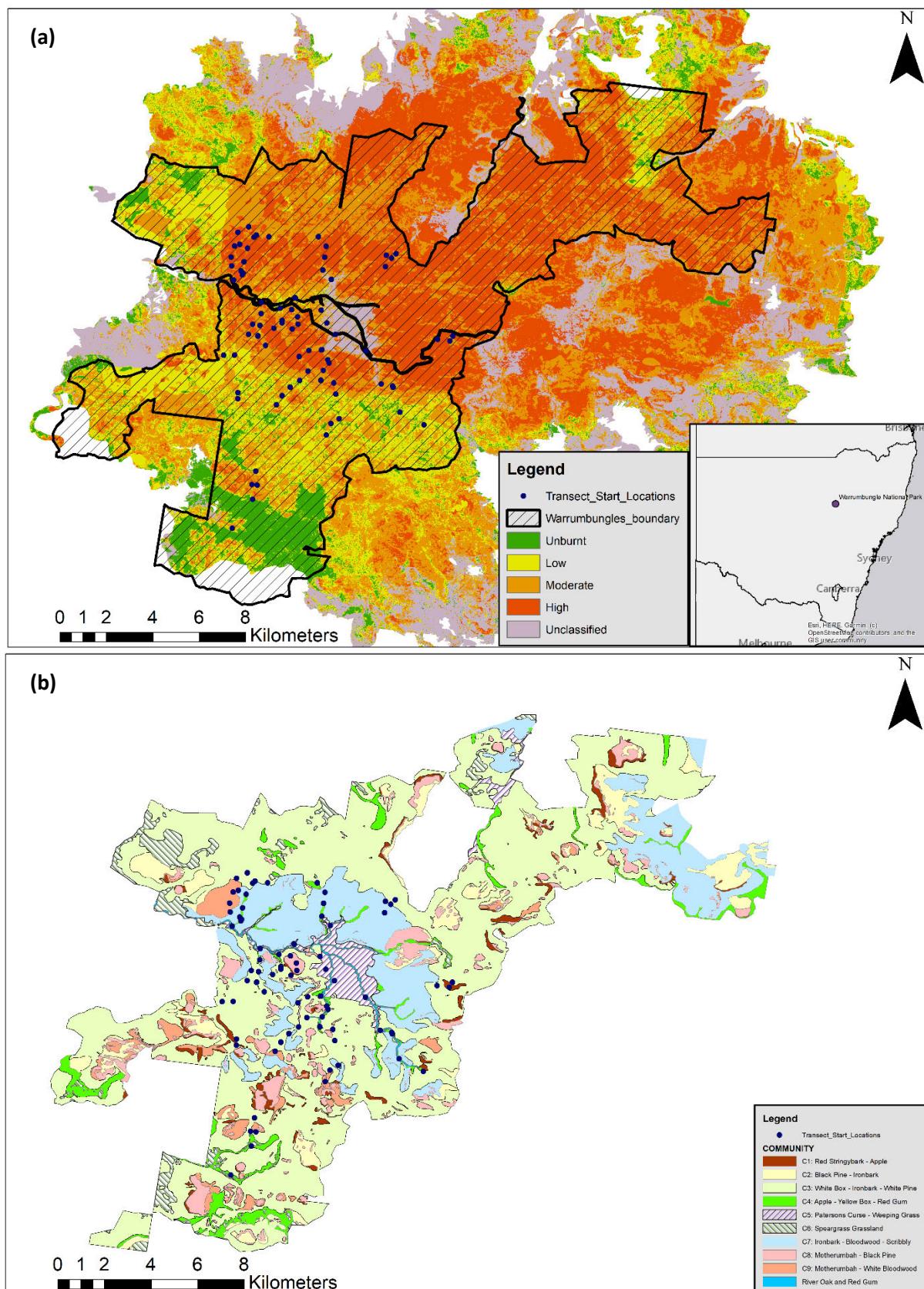


Figure 2. The extent of the Warrumbungle National Park and the location of survey transects, displaying; (a) the extent and fire severity of the 2013 Wambelong fire modified from the Department of Planning and Environment (*unpublished data*); and (b) the ecological communities and associated distribution present within the Warrumbungle National Park, modified from Gordon, Price, Tasker, et al. (2017) and Hunter (2008b)

of a low severity understory burn and grassfire. Due to the hazardous terrain of the WNP transects tended to follow features such as ridgelines, contours, or established trails. Transect locations are depicted in figures 4 & 5.

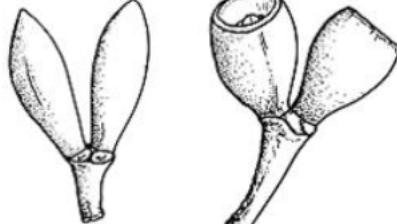
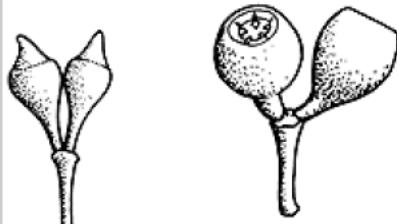
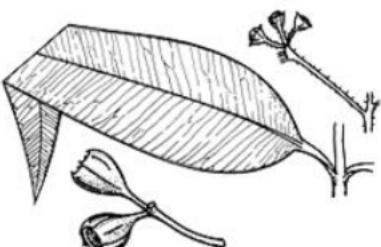
Sampling was conducted by walking the length of each transect. Mistletoe bearing trees were identified visually within a buffer of 10 meters either side of the walked transect. The location of mistletoe bearing host trees was recorded by a Garmin eTrex 20x as a GPS point with a 95% horizontal position error of 3 meters (Garmin Support Center n.d.). For each mistletoe bearing host tree the number of mistletoes members was identified, depicted in figure 3. Living and dead mistletoes are represented as separate data points. This means that trees hosting both living and dead mistletoes were recorded twice. For each surveyed tree that hosted mistletoes, the largest mistletoe member was identified. The height of the mistletoe haustorium perpendicular to the ground was recorded. Mistletoe size was recorded as the vertical * horizontal extent of the mistletoe foliage. Haustoral interface points were only recorded if the remains of the fallen mistletoe could be detected on the ground. This was to prevent the recording of mistletoes that died before the Wambelong fire.



Figure 3. False colour image of the Gunneemooroo survey, depicting Ethan Tsingos (olive), Cameron Kirk (red), and Nathaniel Worcester (orange). Sample tree contains a strong *Amyema miquelii* colony in an *Angophora floribunda*. Note, the large mistletoe immediately above the surveyors was one of two events of hyper-parasitism with an *Amyema miraculosa* (not visible) growing within its foliage. Image Credit: Andrew Denham (2022)

The host tree species was identified based on the colour, texture, and structure of the bark, leaves, and flowering or fruiting bodies. Table 7. provides a list of the commonly found host species and identifiers recorded during the preliminary period, used for the field identification on the main period. Hosts that could not be identified in-situ had images taken of the leaves (where possible) and the bark for later identification. All identification criteria were sourced from personal communications with A. Denham (2022), O. Price (2022), and the Plant Information Network System of The Royal Botanic Gardens and Domain Trust Version 2.0 [online]. In addition, each host tree was given one of five host fire health rating scores based on the dominant form of epicormic regrowth displayed by the tree, outlined in table 8. Unaffected included any trees with minimal or no signs of fire damage from the most recent fire. Branch resprouts included trees with some canopy scorching visible that were dominated by resprouts in the canopy. Trunk resprouts showed signs of heavy canopy consumption and had little of the original canopy surviving. Trunk resprouts could contain some branch resprouting but were dominated by trunk style resprouts. Basal resprouts were trees who displayed signs of complete canopy consumption and had resprouted at or below the soil line. Trees with green foliage or successful resprouts were categorized as dead.

Table 7. The expected common host species within Warrumbungle National Park and identification criteria. Identification images sourced from Harden (1990, 1991) via the Plant Information Network System of The Royal Botanic Gardens and Domain Trust Version 2.0 (National Herbarium of New South Wales)

Host Species	Bark Type	Leaf Type	Identification Image
<i>Eucalyptus albens</i> White Box	Grey w. whitish patches fibrous 'box' type bark. Persistent on lower tree, strips in ribbons higher. Smooth bark beneath.	Blue-green disjunct broad-lanceolate.	
<i>Eucalyptus melliodora</i> Yellow Box	Grey or pale brown fibrous 'box' type bark. Persistent on lower tree, strips in ribbons higher. Smooth bark beneath.	Green or grey-green disjunct narrow-lanceolate.	
<i>Angophora floribunda</i> Rough Barked Apple	Grey short fibrous bark. Bark persistent.	Green lanceolate. Leaves paired on stem.	

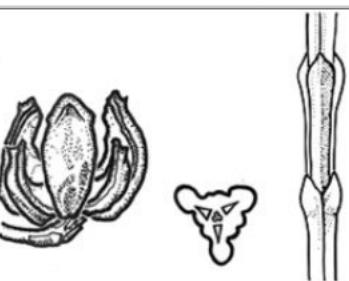
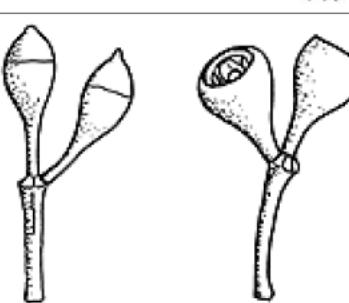
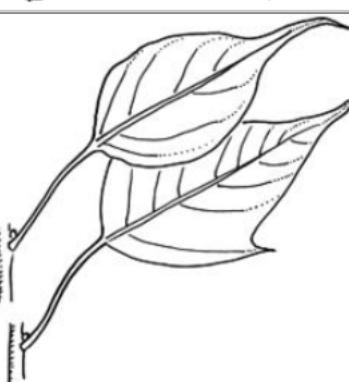
<i>Eucalyptus blakelyi</i> Blakely's Red Gum	Patchy white, grey, brown, and red smooth bark. Bark sheds in large patches and flakes.	Green or grey-green disjunct broad-lanceolate. Leaves alternate on stem.	
<i>Callitris Endlicheri</i> Black Cypress Pine	Brown, tough, deeply furrowed bark.	Narrow coniferous leaves on radial branches.	
<i>Eucalyptus crebra</i> Narrow-leaved Ironbark	Grey-black deeply furrowed 'ironbark' type bark. May have red visible in furrows. Bark persistent.	Dull green to grey-green narrow lanceolate.	
<i>Brachychiton populneus</i> Kurrajong	White fibrous bark. May have traces of green in bark ruts.	Leaves range from ovate (young) to lanceolate (old). Young leaves have distinct three-apex structure. Leaves faintly resemble old-world deciduous trees but are a native evergreen.	
<i>Acacia cheelii</i> Motherumbah	Brown or reddish-brown bark with fine fissures. Can appear flaky or ribbony depending on maturity of plant.	Long elliptic green leaves with closely spaced longitudinal veins. Long, slightly curved pods that appear flat with rounded seed pockets.	

Table 8. The visual indicators of for each host fire health rating and the remotely sensed fire severity associated. Note: non-resprouting trees such as *Callitris endlicheri* can only be categorised as ‘unaffected’ or ‘dead’ by this key. Non-resprouting individuals were always recorded as alive if green foliage was present.

Host Fire Health Rating	Description	Degree of Resprouting	Expected Severity
Unaffected	Host shows superficial or no damage from fire. No sign of epicormic resprout	Original foliage mostly intact. Small degree of regrowth may be present	Unburnt to Low
Branch Resprout	Host shows signs of canopy consumption with epicormic resprouting on terminal branches	Foliage dominated by epicormic regrowth on smaller branches. May have some original foliage or trunk resprout	Low to Moderate
Trunk Resprout	Host shows signs of canopy death with epicormic resprouting on trunk	Foliage dominated by epicormic regrowth on trunk and trunk-like limbs. May have some branch/basal regrowth	Moderate to High
Basal Resprout	Host shows signs of stem death with lignotuber resprouting	Viable foliage present only on branches that originate at or below ground level. Original stem contains no viable foliage	Moderate to High
Dead	Deceased host with no sign of successful resprouting. Fire may not be cause or mortality.	No viable foliage present on host	High*

* May not be indicative of severity

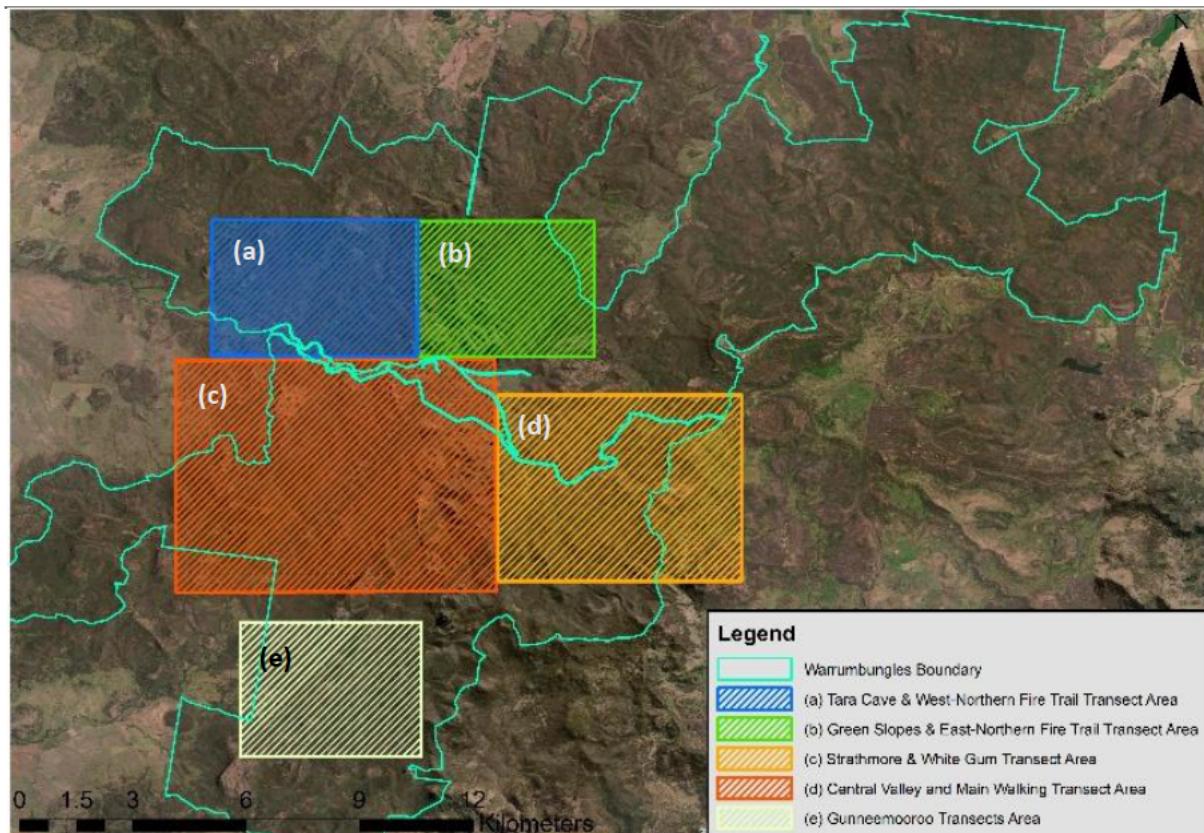


Figure 4. Satellite image of the Warrumbungle National Park depicting the park boundary in light blue and the five transect areas depicted in figure 5.

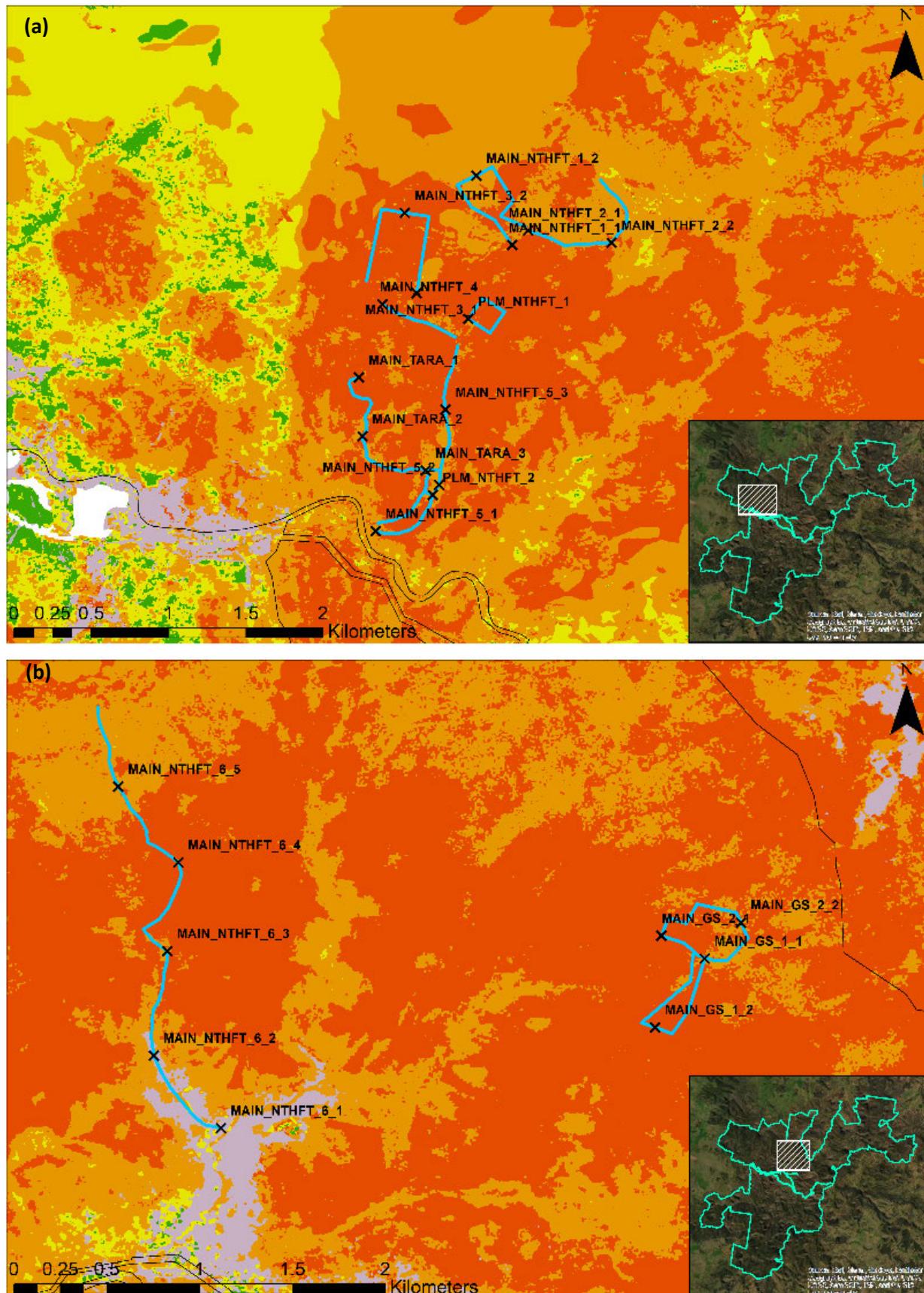


Figure 5. The distribution, direction, and length of the transects at (a) Tara Fire Access Trail and the western extent of the Northern Fire Access Trail, and (b) the eastern extent of the Northern Fire Access Trail and the Green Slopes Fire Access Trail.

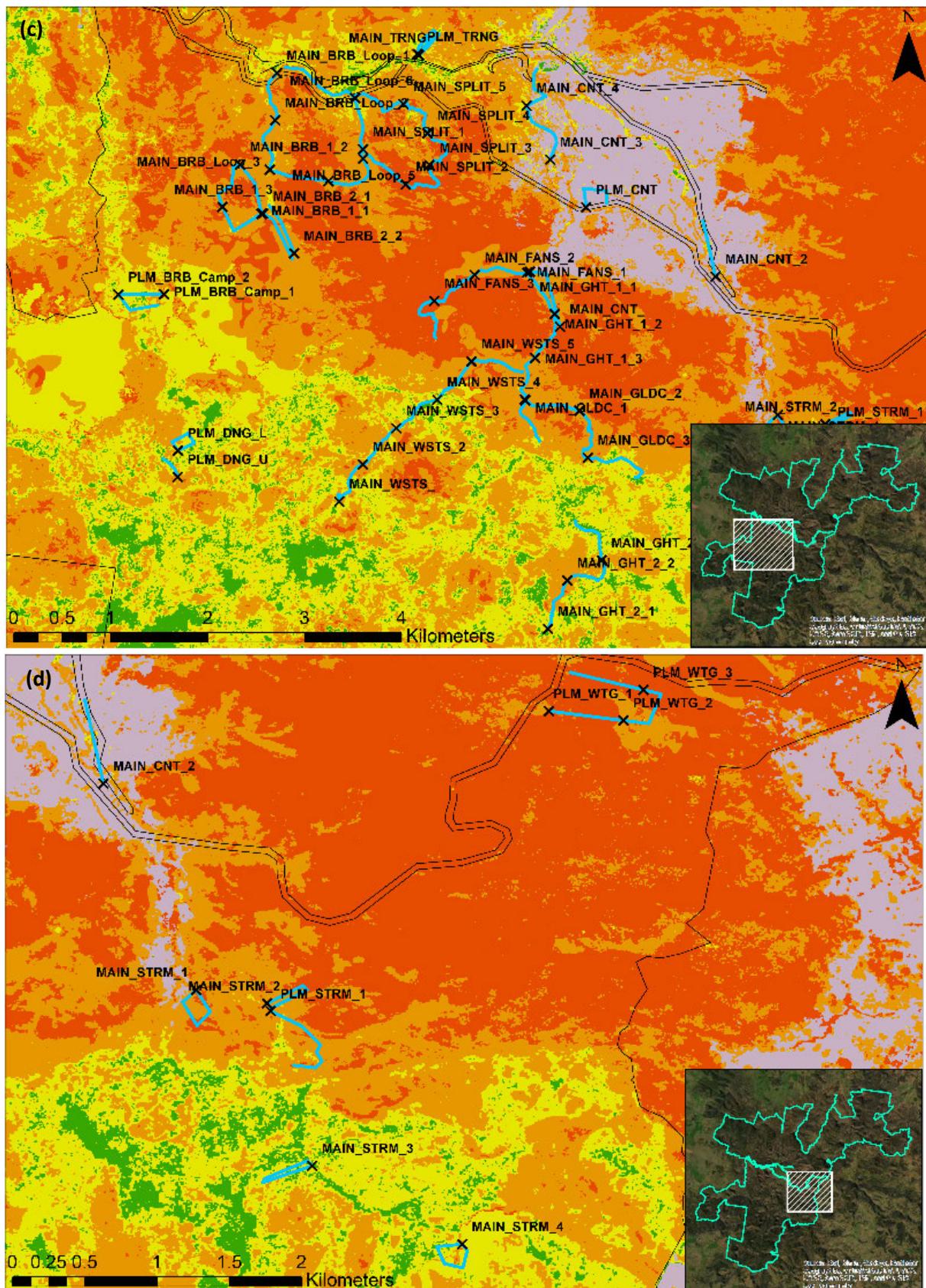


Figure 5. (cont.) The distribution, direction, and length of the transects at (c) Strathmore Fire Access Trail and White Gum Lookout, and (d) the Central Valley, and Main Walking Trails including the Grand High Tops, Split Rock, and Burbie Fire Trail,

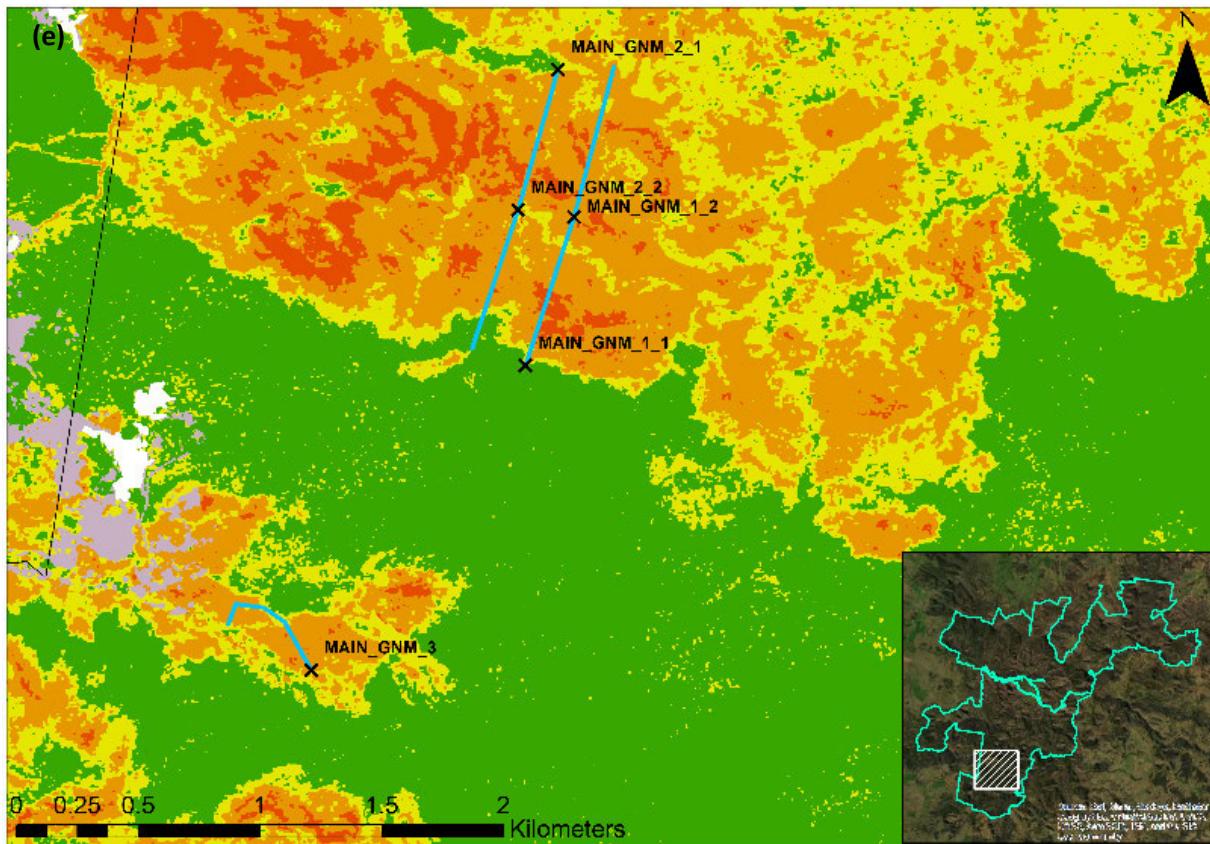


Figure 5. (cont.) The distribution, direction, and length of the transects conducted at (e) Gunneemooroo Fire Trail. Transects overlay the fire severity map modified from Department of Planning and Environment (*unpublished data*)

3.2 Analysis

The analysis was performed at two scales, the individual mistletoe scale and the transect scale. To test the effects of high severity fire on mistletoe several predictor variables have been assessed to determine the survival rate response variables. All statistical testing was completed within the base packages of RStudio 1.3.1093.

Model analysis was performed through a combination of Null probability (P), McFadden's pseudo-R-Squared (R^2), and Akaike's information criterion (AIC). Null probability was validated against a significance level (α) of 0.05. Pseudo-R-squared methods for binomial regression are analogous to R-squared for linear models but differ in their functionality. (McNulty 2021). R^2 was calculated through McFadden's pseudo-R-squared formula $R^2_{Adj} = 1.0 - \frac{\ln(L) - K}{\ln(L_0)}$, which compares a likelihood function of the fitted and null model to estimate the variance (McNulty 2021). Pseudo-R-squared is not a direct goodness-of-fit but provides information regarding the model with the greatest likelihood of explaining the variance (McNulty 2021). McFadden's pseudo-R-squared method produces considerably lower values than a linear R^2 index with values between 0.2 to – 0.4 representing an excellent fit (McFadden 1979). AIC is a relative measure that compares multiple models among candidates to inform the best suited model but does not measure model fit (Symonds & Moussalli 2011)

Binomial family generalized linear models with the logit link function were used to investigate the effects of multiple predictor values on the response variable of mistletoe survival:

1. Survival of individual mistletoes with remotely sensed fire severity as the predictor,
2. Survival of individual mistletoes with field observed host fire health rating as the predictor,
3. Survival rate of the largest mistletoe for each host with mistletoe height as the predictor
4. Survival rate of the largest mistletoe for each host with mistletoe size as the predictor
5. Survival rate of a mistletoe colony with the host species as the predictor
6. Survival rate of a mistletoe colony with the host ecological community as the predictor.

Additionally, a Gaussian family generalized linear model with the identity link function was used to assess the survival rate of mistletoes by the mean transect severity.

7. Transect survival rate of mistletoes with the transect mean fire severity as the predictor.

Transect mean fire severity was determined using ArcMap 10.7.1 through a 10-meter buffer either side of each transect. Mean fire severity was determined by averaging the area of each fire severity in the buffer. Transects with no mistletoes were excluded from the GLM to prevent potential biases caused by areas with no historic mistletoe infections prior to the Wambelong fire.

Chapter 4. Results:

The survey identified 1209 unique mistletoes, representing 574 living and 635 dead mistletoes. The mistletoes were sampled across all four severity categories, including 160 mistletoes in unburnt severity, 519 mistletoes in low severity, 477 mistletoes in moderate severity, and 53 mistletoes in high severity. The mistletoes represented six identified species, representing two mistletoe families. Loranthaceae species identified included *Amyema bifurcata*, *Amyema miquelii*, *Amyema miraculosa*, *Amyema pendula*, and *Muellerina bidwilli*. *Notothixos cornifolius* was the only identified species of the Viscaceae family. *A. miraculosa* represents the only species of mistletoe that had not previously been documented within the Warrumbungle National Park (Hunter 2008a; NSW Department of Planning and Environment et al. 2022). A total of 17 host species were identified (Table 9.). This included 15 hosts representing trees or shrubs, and 2 events of mistletoe hyper-parasitism. *A. bifurcata* and *A. miquelii* were both observed as viable hosts for mature and flowering *A. miraculosa* specimens. For the data analysis, the tree species was used for events of hyper-parasitism rather than the host. Two identified mistletoes have been excluded from the dataset. A combination of the vertical extent, horizontal extent, height, and host fire health rating suggested that the two datapoints were a sampling error and have been removed from the results as an outlier.

Table 9. The frequency of mistletoe hosts found within the Warrumbungle National Park. Hosts marked with ‘*’ represent hyper-parasite hosts and have not been used for the statistical analysis models.

Host Species	Common Name	Host Frequency
<i>Acacia cheelii</i>	Motherumbah	1
<i>Acacia deanei</i>	Deane's Wattle	2
<i>Amyema bifurcata</i>	Forked Mistletoe	1*
<i>Amyema miraculosa</i>	Fleshy Mistletoe	1*
<i>Angophora floribunda</i>	Rough-barked Apple	118
<i>Brachychiton populneus</i>	Kurrajong	14
<i>Casuarina cunninghamiana</i>	River She-oak	1
<i>Callitris (endlicheri and glauköphylla)</i>	Cypress Pine	46
<i>Corymbia trachyphloia</i>	Brown Bloodwood	8
<i>Eucalyptus albens</i>	White Box	147
<i>Eucalyptus blakelyi</i>	Blakely's Red Gum	106
<i>Eucalyptus crebra</i>	Narrow-leaved Ironbark	48
<i>Eucalyptus dealbata</i>	Tumbledown Red Gum	2
<i>Eucalyptus macrocarpa</i>	Red Stringybark	3
<i>Eucalyptus melliodora</i>	Yellow Box	50
<i>Eucalyptus racemosa</i> subsp. <i>rossii</i>	Inland Scribbly Gum	10
<i>Santalum acuminatum</i>	Desert Quandong	2

The thesis surveyed 44005 meters of transect covering a buffered survey area of 83.71 ha. Increasing severity was associated with decreasing mistletoe abundance for living, dead and total mistletoes. 2.09 ha of unburnt severity was sampled with a total mistletoe abundance of 76.6/ha, a live mistletoe abundance of 53.2/ha, and a dead mistletoe abundance of 23.5/ha. 12.37 ha of low severity was sampled with a total mistletoe abundance of 42.0/ha, a live mistletoe abundance of 24.6/ha, and a dead mistletoe abundance of 17.4/ha. 43.2 ha of moderate severity was sampled with a total mistletoe abundance of 11.0/ha, a live mistletoe abundance of 3.52/ha, and a dead mistletoe abundance of 7.52/ha. 26.0 ha of high severity was sampled with a total mistletoe abundance of 2.04/ha, a live mistletoe abundance of 0.269/ha, and a dead mistletoe abundance of 1.77/ha.

Increasing fire severity was associated with a decrease in mistletoe observed survival rate. Mistletoes in unburnt severity had an observed survival of 69.4% with 111 live individuals and 49 dead individuals. Mistletoes in low severity had an observed survival of 58.6% 304 live individuals and 215 dead individuals. Moderate severity had an observed survival of 31.7% with 152 live and 325 dead individuals. High severity had an observed survival of 13.2% with 7 live and 46 dead individuals. The seven living mistletoes in high severity area were distributed across four living hosts. One of the hosts was unaffected by the fire and three of the hosts had epicormic regrowth in the terminal branches. All four host trees are located on a boundary pixel showing they are within 5 meters of a lower severity class. Fire severity uses a sample population of 1209 individual mistletoes. The model 1 GLM (Table 10. & Figure 6a.) found fire severity to be a strong survival predictor with a *P* value of < 0.01 . This rejects the null hypothesis that severity does not affect the survival of mistletoes. Model 1 had an R^2 value of 0.0759 showing a large deviation between the model prediction and the observed data. Model 1 outputs a predicted survival rate of 75.3% for unburnt areas, showing a slight overestimation compared to the observed survival. The model outputs predicted survival of 55.3% for low severity and 33.3% for moderate severity showing a marginal deviation from observed survival at these severities. Model 1 predicted survival for high severity is 16.8% which represents a considerable overestimation of ~26% when compared to the observed survival.

Increasing host fire health was associated with a strong decline in observed survival. Individuals on unaffected trees had an observed survival of 63.1% with 398 live individuals and 223 dead individuals. Mistletoes on branch resprouting trees had an observed survival of 42.7% with 175 live individuals and 235 dead individuals. Mistletoes on trunk resprouting trees had a 2.63% observed survival with 1 live individual and 37 dead individuals. Basal resprouting hosts had an observed survival of 0% with 40 dead individuals. Dead hosts also recorded an observed survival of 0% with 65 dead individuals. Model 2 used a sample population of 1209 individual mistletoes. The model 2 GLM (Table 11. & Figure 6b.) found host fire health to be a strong survival predictor with a *P* value of < 0.01 . This rejects the null hypothesis that host fire health does not significantly affect the survival of individual mistletoes. Model 2 had an R^2 value of 0.13. The R^2 value decreases to 0.1287 for model 2 when the GLM is calculated

Table 10. Model 1 outputs for the generalized linear model predicting mistletoe health from fire severity

	Estimate	Std. Error	Z Value	P	
<i>Intercept</i>	1.12019	0.13017	8.606	< 2e-16	
<i>Severity</i>	-0.91122	0.08627	-10.563	< 2e-16	
Null Dev.	1673.0	Residual Dev.	1545.9	AIC	1554.9

Table 11. Model 2 outputs for the generalized linear model predicting mistletoe health from host fire health rating

	Estimate	Std. Error	Z Value	P	
<i>Intercept</i>	0.63135	0.07937	7.955	1.79e-15	
<i>Fire Rating</i>	-1.17967	0.09953	-11.853	< 2e-16	
Null Dev.	1673.0	Residual Dev.	1427.8	AIC	1431.8

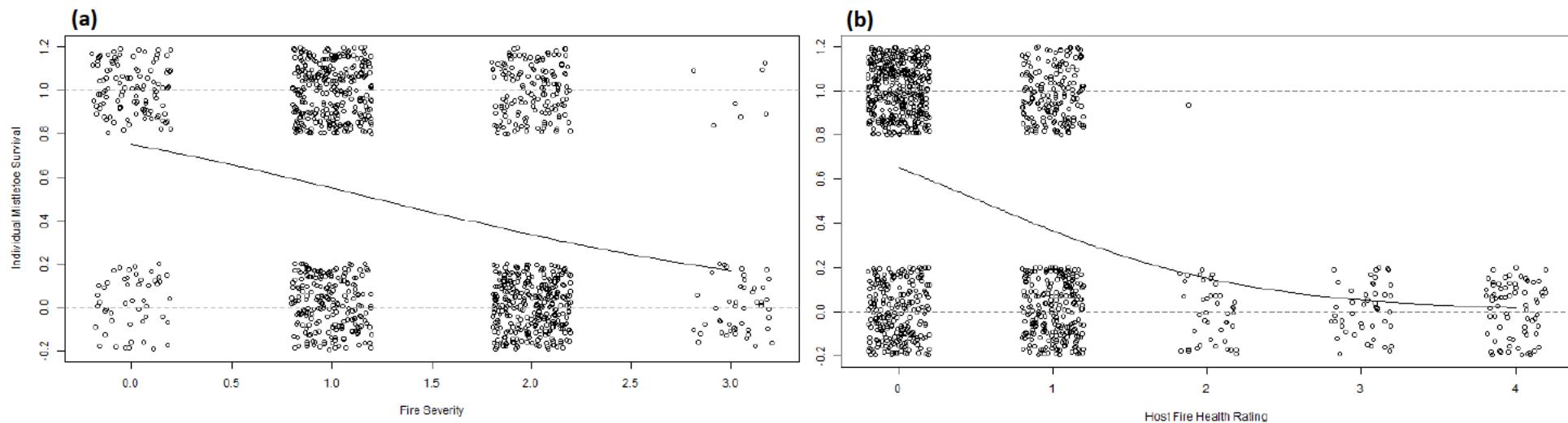


Figure 6. The survival rate of individual mistletoes as a function of (a) fire severity, and (b) host fire health rating. Regression lines represent the model survival prediction generated by GLMs. (a) Fire Severity values represent: 0. Unburnt, 1. Low, 2. Moderate, & 3. High. (b) Host Fire Health Rating values represent: 0. Unaffected, 1. Branch resprouting, 2. Trunk resprouting, 3. Basal resprouting, & 4. Dead. Data clusters have been jittered on the x and y axis to represent the concentration of data values on each point.

Table 12. Model 3 outputs for the generalized linear model predicting the largest mistletoe health from mistletoe height

	Estimate	Std. Error	Z Value	P	
Intercept	-0.72168	0.16838	-4.286	1.82e-05	
Height	0.02278	0.01317	1.730	0.0836	
Null Dev.	742.99	Residual Dev.	740	AIC	744

Table 13. Model 4 outputs for the generalized linear model predicting the largest mistletoe health from mistletoe area

	Estimate	Std. Error	Z Value	P	
Intercept	-0.9571	0.1171	-8.172	3.03e-16	
Area	0.4129	0.0693	5.958	2.55e-09	
Null Dev.	742.99	Residual Dev.	690.73	AIC	694.73

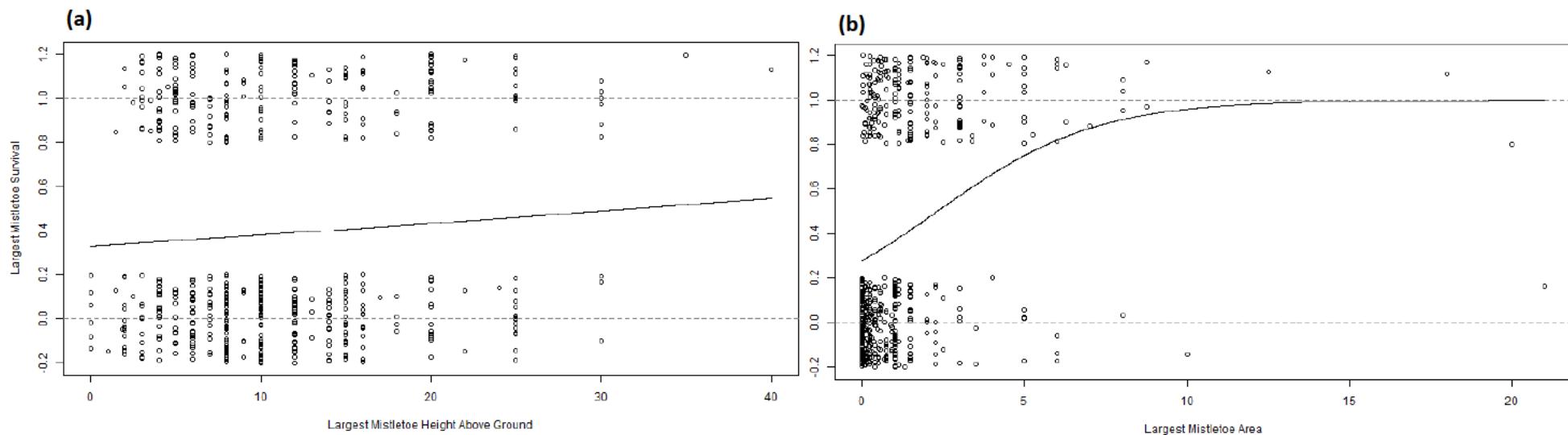


Figure 7. The survival rate of the largest mistletoe for each host as a function of (a) haustorium height above ground level, and (b) size, represented by an approximated cross-sectional area, of the mistletoe. Regression lines represent the model survival prediction generated by the GLMs. Data clusters have been jittered on the y axis to represent the concentration of binary survival values at each x value

with the basal outliers included. Model 1 has an AIC of 1549.9 while model 2 has an AIC of 1431.8 for 1209 datapoints. The 0.134 R² of model 2 is a significant increase in when compared to the 0.0759 R² of model 1. The 123.1 reduction in AIC and increase in R² shows that model 2 fits the observed data better and explains a larger portion of the deviation in the model.

The height of the haustorium above ground level was a weak predictor for the survival rate of the largest mistletoe for each host. An apparent relationship was observed for with a low 27.3% observed survival for near-ground (less than 2 m) and a 72.7% observed survival for high-canopy (30 m or greater). However, when the entire sample population is considered, no statistically significant relationship is observed. Model 3 uses a sample population of 558 mistletoes. The model 3 GLM (Table 12. & Figure 7a.) was a weak survival predictor with a P value of 0.0836 and an R² value of 0.004. This P value is greater than the α of 0.05 and is insufficient to reject the null hypothesis that height has a significant effect on the survival rate of mistletoes. Model 3 was redesigned to test the effect of height at low severity. Model 3b recalculated model 3 with unburnt and low severity mistletoes, excluding higher severity mistletoes. Model 3b was also unable to reject the null hypothesis with an insignificant P value of 0.395 and R² value of 0.0001.

The size of the mistletoe was a strong predictor for the survival rate of the largest mistletoe for each host. There is a marked increase in the average size of surviving mistletoes for both mean and median methods. The mean size for a surviving mistletoe was 1.97 m² compared to the mean dead size of 0.776 m². The median size for a surviving mistletoe is 1.13 m² compared to the median dead size of 0.25 m². As the data has a strong positive distribution skew it has been represented normally (Figure 7b.) and with a log transformation (Figure 8.) Small mistletoes (1 m² and under) had a low observed survival of 26.0%, while mid-range mistletoes (between 1 m² and 5 m²) had an observed survival 54.5%, and large mistletoes (5 m² and above) had an observed survival of 72.4%. Model 4 has a sample population of 558 mistletoes. The model 4 GLM (Table 13. & Figure 7b.) was a strong survival predictor with a P value of < 0.01 and R² value of 0.0703. This rejects the null hypothesis that mistletoe size does not significantly affect the survival rate of mistletoes.

For host species a reduced dataset was used to determine the survival of a mistletoe colony. Species with host frequency < 40 were excluded from the dataset. The reduced sample population included 465 host trees. Host species was found to be a strong predictor of mistletoe survival. The model 5 GLM (Table 14.) had a low R² value of 0.0438. 3 host species had statistically significant changes in survival. *Callitris* had 11 living colonies and 35 dead colonies. This gives it a P value of < 0.01 and an observed survival of 23.9%. *E. blakelyi* had 31 living colonies and 75 dead colonies. This gives it a P value of < 0.01 and an observed survival of 29.2%. *E. crebra* was the final statistically significant species with 11 living colonies and 37 dead colonies. This gives it a P value of < 0.01 and an observed survival of

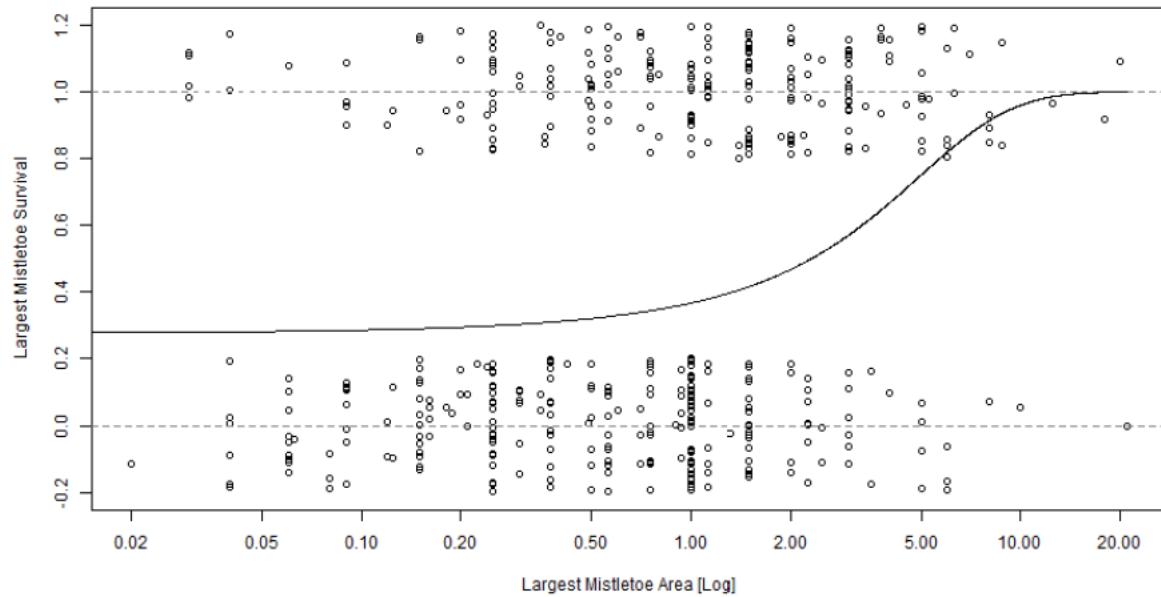


Figure 8. The survival rate of the largest mistletoe for each host by the logarithmic cross-sectional area of the largest mistletoe. Regression line represents the model 4 GLM. Data has been jittered on the y axis to represent the concentration of binary survival values at each x value.

Table 14. Model 5 outputs for the generalized linear model predicting the survival of a mistletoe colony from host species with sample sizes greater than 40 mistletoe colonies.

	Estimate	Std. Error	Z Value	P	
<i>A. floribunda</i>	0.1018	0.1844	0.552	0.580875	
<i>Callitris</i>	-1.2592	0.3917	-3.214	0.001307	
<i>E. albens</i>	-0.2244	0.2476	-0.906	0.364784	
<i>E. blakelyi</i>	-0.9853	0.2821	-3.493	0.000478	
<i>E. crebra</i>	-1.3148	0.3898	-3.373	0.000743	
Null Dev.	624.24	Residual Dev.	596.91	AIC	606.91

Table 15. Model 6 outputs for the generalized linear model predicting the survival of a mistletoe colony from host ecological community with sample sizes greater than 40 mistletoe colonies

	Estimate	Std. Error	Z Value	P	
<i>C3</i>	-0.4019	0.1340	-3.000	0.0027	
<i>C4b</i>	-0.5144	0.2607	-1.973	0.0484	
<i>C5</i>	0.2894	0.2511	1.153	0.2490	
<i>C7a</i>	-0.4132	0.2672	-1.546	0.1220	
Null Dev.	670.70	Residual Dev.	661.31	AIC	669.31

22.9%. These statistically significant host species suggest a rejection of the model null hypothesis that host species has no effect on mistletoe colony survival. For host ecological community a reduced dataset was used to determine the survival of a mistletoe colony. Ecological communities with community frequency of < 40 were excluded from the dataset. The reduced dataset has a sample population of 507 host trees. Ecological community was found to be a strong predictor of mistletoe survival. The model 6 GLM (Table 15.) had a moderate R^2 of 0.0140.



Figure 9. One of the two juvenile *Amyema miraculosa* found parasitising a young *Acacia deanei* showing the undeveloped, long root-like haustorium rather than the characteristic bulb-like holdfast of mature mistletoes. Image has been marginally false-coloured to increase the contrast between mistletoe and host plant. Image Credit: Cameron Kirk (2022)

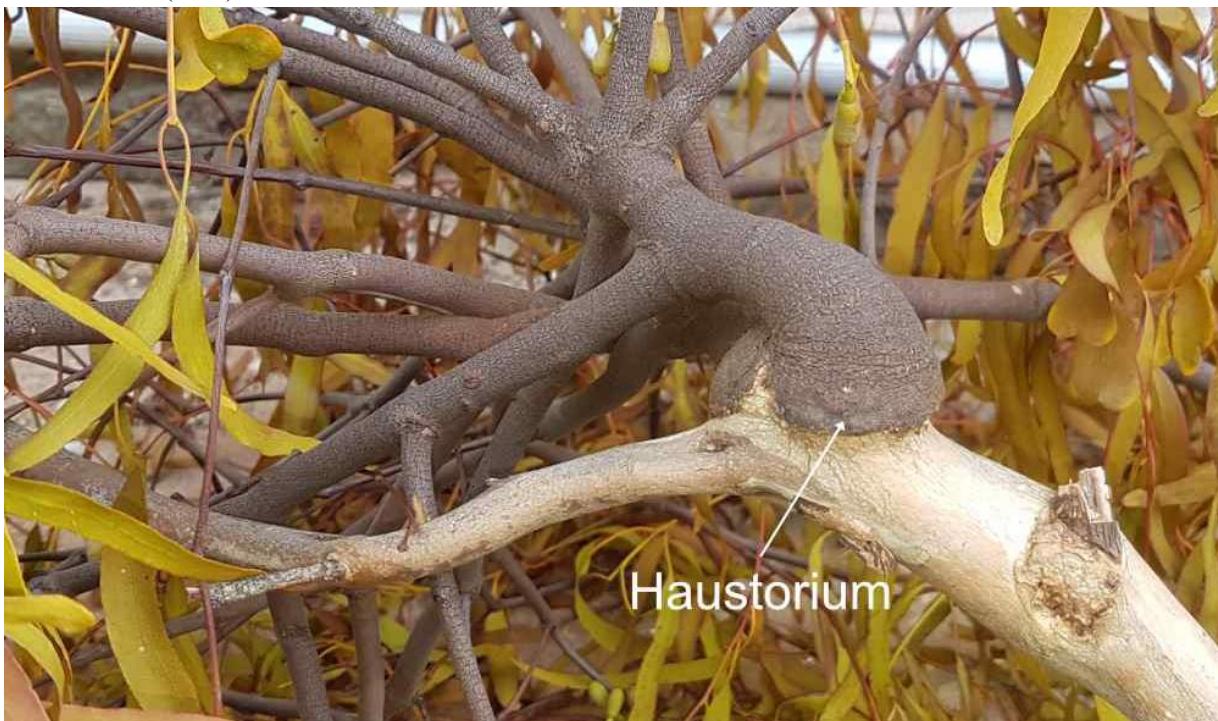


Figure 10. A mature *Amyema miquelii* parasiting a *Eucalyptus wandoo* branch labelling the developed bulb-like haustorium structure characteristic of mature *Amyema* mistletoes. Image Credit: Doug Swakins (2012)

Two ecological communities had statistically significant changes to survival. C3: White Box - Ironbark - White Pine had 93 living and 139 dead mistletoe colonies. This presents a P of 0.002 and an observed survival of 40.1%. C4b: Apple - Yellow Box - Red Gum had 28 living and 70 dead mistletoe colonies. This presents a P of 0.048 and an observed survival of 28.6%. These ecological communities suggest a rejection of the model null hypothesis, ecological community does not affect mistletoe colony survival.

Increasing transect severity was associated with a decrease in transect observed survival (Figure 11.). Of the 81 transects used for the survey, 59 transects contained mistletoes and 22 transects contained no detected mistletoes. Of the 59 transects where mistletoes were observed, 25 transects contained living mistletoes. The model 7 GLM (Table 18.) found that mean transect severity was a strong transect survival predictor with a P value of < 0.01 and an R^2 value of 0.2950. This rejects the null hypothesis that mean transect fire severity does not significantly affect the survival of observed mistletoes. Figure 12. depicts the distribution of transects across the survey area showing the near 0 observed survival of transects in the moderate to high severity region in the central, northern, and eastern extent of the park. An area in the middle of the park containing the Central Valley and Wambelong Creek had predominantly higher observed survival transects ($>30\%$ observed survival). This is notable as the area is surrounded by high severity to its north, east, and south. This area has been heavily disturbed from historic land clearing and John Renshaw Parkway. The southern region of the park is characterized by a variable severity dominated by low and moderate severity areas with isolated pockets of unburnt or high severity. This area is predominantly higher observed survival transects. The model 7 GLM (Table 16.) had a significant P value of < 0.01 and a moderate R^2 of 0.295. This rejects the null hypothesis that transect mean severity does not correlate to observed mistletoe survival rate.

Table 16. Model 7 outputs for the gaussian linear model predicting the survival rate of mistletoes along a transect based on the mean fire severity of the transect, averaged from the area of a 10-meter buffer either side.

	Estimate	Std. Error	t Value	P
Intercept	0.77398	0.11578	6.685	1.07e-08
Mean Severity	-0.25940	0.05312	-4.884	8.81e-06
Null Dev.	5.5280	Residual Dev.	3.8974	AIC 13.118

Of the 576 living mistletoes identified by the survey, only 2 individuals were identified as mistletoes that had established post-fire. Both individuals were identified as *A. miraculosa* and were found on separate *Acacia. deanei* hosts within 20 meters of each other at the southern end of the MAIN_GNM_2_2 transect. Both mistletoes were identified as juvenile based on the lack of developed haustorium connection, seen in figure 6. The root like attachment structure of young hosts is distinct from the large bulb characteristic of a mature mistletoe, seen in figure 7. Both hosts were spatially distributed in an unburnt fire severity region on the rDNDVI map. Both hosts were identified as unaffected by the fire but were noted as potentially younger than the fire based of their size. Nearby host trees were labelled as a mixture of unaffected and branch resprouts suggesting the area was affected by low severity fire.

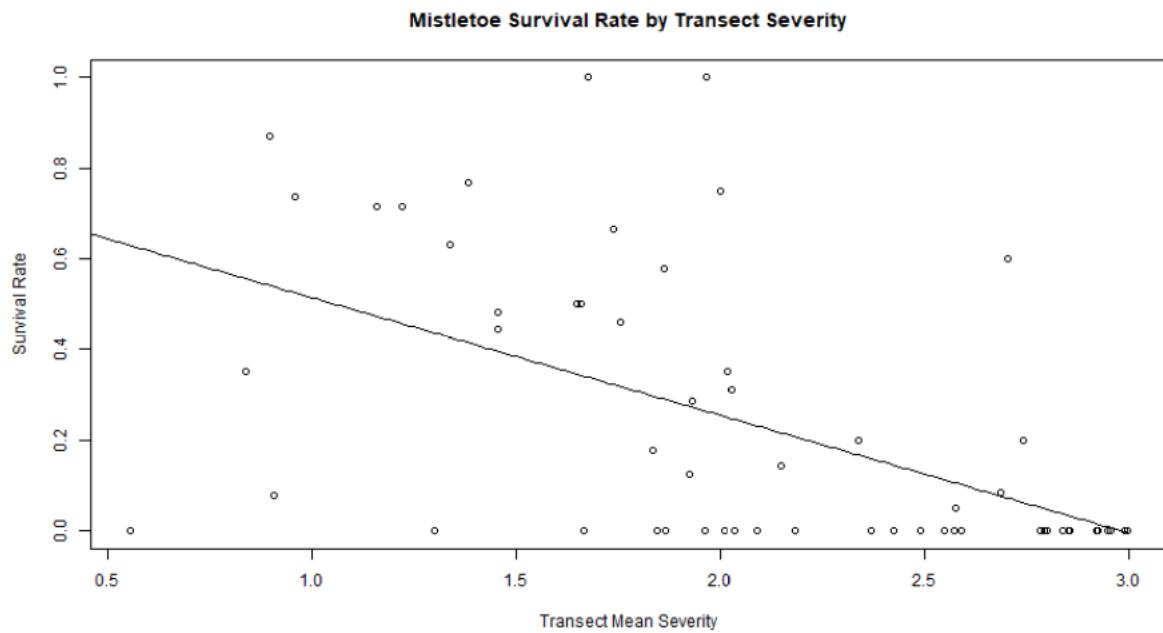


Figure 11. Scatterplot of the survival rate of individual mistletoes for each transect of the survey. Transects with no living or dead mistletoes present are excluded from the graph. Regression line represents the gaussian GLM survival rate prediction.

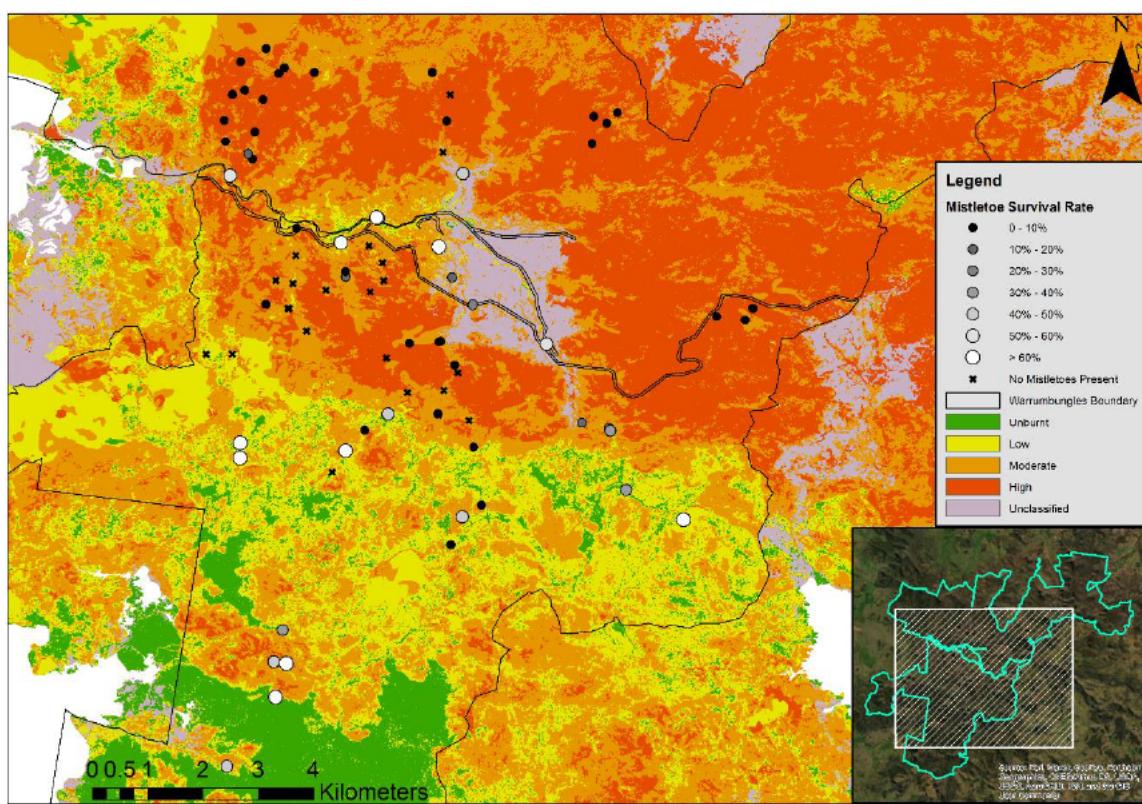


Figure 12. Focused map of the survey area within the WNP showing the distribution of transects and associated mistletoe survival rate. Transects with no mistletoes present are denoted by 'x' symbols. Points represent the starting location for the transect.

Chapter 5. Discussion

This thesis was designed to advance the understanding of Australian mistletoe ecology by examining the interactions between high severity fire and mistletoes. This includes the degree of mortality caused by increasing fire severity, and the processes by which mistletoes recolonise high severity areas. This thesis also has broader implications for ecology as an example of how a fire vulnerable obligate colonisers can persist in environments within a regime of high severity fires.

The thesis aimed to quantify the relationship between remotely sensed fire severity and mistletoe survival in the dry sclerophyll forest of the Warrumbungle National Park and use this to develop a predictive model for application in future fire events. Previous studies in Australia have assessed the effect of fire regime on the distribution and biodiversity of mistletoes (Start 2011, 2013, 2015) and the effectiveness of selective burning of mistletoes as a way to treat mistletoe infections (Kelly et al. 1997) but no studies have quantified the effects of fire severity on mistletoe survival. It was predicted that increasing fire severity would correlate to decreasing mistletoe survival. This thesis supports the hypothesis with the greatest observed survival rate in unburnt severity areas and the lowest survival rate in high severity areas. It was also predicted that increasing host fire health would correlate with decreasing mistletoe survival. This was supported by the thesis with the greatest observed survival rate for unaffected hosts and no survival rate for basal resprouts or dead hosts.

The thesis was additionally designed to quantify the effects of a broader range of variables that may affect mistletoe survival including mistletoe height, size, host species, and host ecological community. It was proposed that increasing mistletoe height and size would increase the survival rate of mistletoes. The thesis supported the hypothesis that increasing mistletoe size increases survival rate with the highest survival rate being observed for large mistletoes of 5m² and larger. The thesis did show a weak relationship between mistletoe height and survival, but the predictive power of the relationship was not strong enough to reject the null hypothesis that mistletoe height does not affect survival. It was predicted that host species and host ecological community would vary the survival rate of mistletoes. The thesis supports the hypothesis that host species can affect the survival rate of mistletoes. The thesis also supports the hypothesis that host ecological community can affect the survival rate of mistletoes. Host species is a better determinant of survival for field-based surveys but host ecological communities would provide an adequate predictor for remote survival assessment.

The final purpose of the thesis was to inform the Department of Planning and Environment on the effect of the Wambelong fire on the distribution of mistletoe populations within the Warrumbungle National Park. By analysing the survival rate per transect, a pattern was observed where the large higher severity area in the central, north, and eastern extent of the park was dominated by 0-10% survival transects. The southern mixed severity area of the park was predominantly >20% survival transects, and the area

along the Central Valley and Wambelong Creek was predominantly >50% survival transects. This shows that mistletoes are absent from a large portion of the park where higher severities of fire were dominant. However, strong mistletoe populations still exist in the Central Valley, Wambelong Creek, and the southern extent of the park that would allow for the recolonisation of the higher severity areas through edge recruitment. Almost no sign of recolonisation was apparent 9 years after the fire, suggesting that it may be a multi-decadal process similar to the recovery of other fire vulnerable species like *Callitris*.

5.1 Mistletoe Survival from Fire Characteristics

Fire severity is the measure of the ecological impact of a fire determined by the consumption of biomass in a vertical plane of reference (Etchells et al. 2020). Mistletoes, as aerial habit plants, typically inhabit higher strata in a forest structure. Mortality rates for mistletoes exposed to direct flame for at least 20 seconds exceeds 50%, showing that 20 seconds of flame immersion is enough to induce the instantaneous lethal temperature of 64°C for mistletoe tissue (Kelly et al. 1997). While some species of Australian mistletoe have been shown to be capable of resprouting from scorched haustorial tissue following total canopy scorch (Start 2015) this has not been demonstrated for any species listed in the WNP. This indicates that mistletoes would be least affected by low severity burns that consume the understory of a forest, and most affected by moderate to high severity burns characterised by the scorching or consumption of the canopy. This would immerse the mistletoe strata in flame with the potential to bring subcortical buds to the lethal temperature. This thesis found that the observed survival rate of mistletoes decreased from 58.6% across low severity burn areas to 31.9% in moderate severity and 13.2% in a high severity burn areas. This represented a marked decrease in the survival rate of mistletoes across all fire severities from the baseline of unburnt forest of 69.4%. This affirms the hypothesis that mistletoe survival rate responds negatively to increasing severity. The decrease in survival rate for low severity burns is noteworthy as previous research had suggested, but not confirmed, that even low severity burns may generate enough heat to scorch low canopy mistletoes (Kelly et al. 1997). It was expected that the crown scorch during high severity fire would kill all mistletoes as suggested by similar studies (Kelly et al. 1997; Start 2015). This presumption was not supported by the observed survival rate with seven living mistletoes distributed through four hosts in high severity area. Three of the four hosts exhibited some degree of canopy scorch but had established epicormic regrowth on the terminal branches, the remaining host exhibited only superficial damage from the fire. All four hosts are spatially located on high severity pixels adjacent to lower severity classes. This suggests that their classification as high severity mistletoes resulted from the misclassification of fire severity from the rDNDVI classification. Field validation studies for rDNDVI have found it's balanced accuracy with field observations ranges from 52.9% to 80.7% with a 77.3% accuracy for high severity (Gibson et al. 2020). This suggests that systematic error due to remotely classified fire severity is likely to be recurrent in subsequent studies, however the use of a combination reflectance and fractional cover model can

increase the balanced accuracy significantly (Gibson et al. 2020). As the systematic error is likely to be recurrent in subsequent studies the high severity survivors have not been treated as outliers.

The analysis of transect severity also supported the hypothesis that mistletoe survival rate responds negatively to increasing severity. Transect severity was a strong predictor but suffered a high degree of deviance when predicting the survival rate of mistletoes observed on the transect. This deviance largely comes from several low severity transects with 0 survival rate that skew the model in favour of underestimating transect survival at lower severities. This large degree of survival variation in lower transects suggests that other factors may have contributed to the low survival rate of mistletoes in these areas. Mistletoes have been observed to prematurely die during prolonged drought events where the host persists (Crates et al. 2022; Watson 2015). The WNP suffered a short but severe drought during 2017-2019 (Stevens & Watson 2022) that may have contributed to mistletoe death.

Additionally, I propose that the methodology used for this thesis superficially inflates the survival rate of mistletoes for two reasons. The first reason was the exclusion of observed haustorium interface points from the survey. Mistletoes are commonly shorter-lived than their hosts so it is common to observe mistletoe senescence resulting in the falling of the mistletoe body from the host tree (Start 2011). Other factors such as drought would contribute to pre-fire senescence. It was observed during the thesis that the interface point of the mistletoe haustorium can leave a swollen growth on the host, depicted in figure 13. This growth can be identified on some hosts where senescence had occurred, and the mistletoe body was indetectable. There was no practical way to distinguish a haustoral interface of a mistletoe that died before, during, or after the fire. Thus, to avoid biases from recording pre-fire dead mistletoes, mistletoes where the only surviving evidence was the haustoral interface were excluded. This prevents the inclusion of pre-fire mortality mistletoes but is also likely to exclude mistletoes that died because of the fire and senesced or were consumed by the fire leaving only the haustorium. The second reason is the destruction of mistletoe evidence during and following high severity fire. I propose that the consumption of the host tree terminal branches during the fire, the shedding of dead branches and treefall following the fire would eliminate most evidence of historic mistletoe infections. This bias is illustrated in figure 14. This may explain the reduction in mistletoe abundance observed with increasing fire severity, suggesting that the population of dead mistletoes in higher severity areas was higher than observed.

The difference in the observed mistletoe abundance was greatest between unburnt and high severity areas, with observed abundance decreasing by 97.3% in high severity areas when compared to unburnt areas. This can be corrected for by extrapolating the mistletoe abundance of unburnt fire severity to determine the number of expected post-fire mistletoes. Unburnt severity had an observed mistletoe abundance of 76.9/ha. From this an abundance corrected survival was estimated by comparing the number of observed mistletoes to the number of expected pre-fire mistletoes. Low severity represented



Figure 13. The large swollen growth on a *Brachychiton diversifolius* at the haustoral interface of a *Notothixos cornifolius* ‘Kurrajong Mistletoe’ that can remain present on the host tree long after the death and fall of a mistletoe body. Image Credit: Jill Newland (2009), sourced from Fryer and Newland (2017)

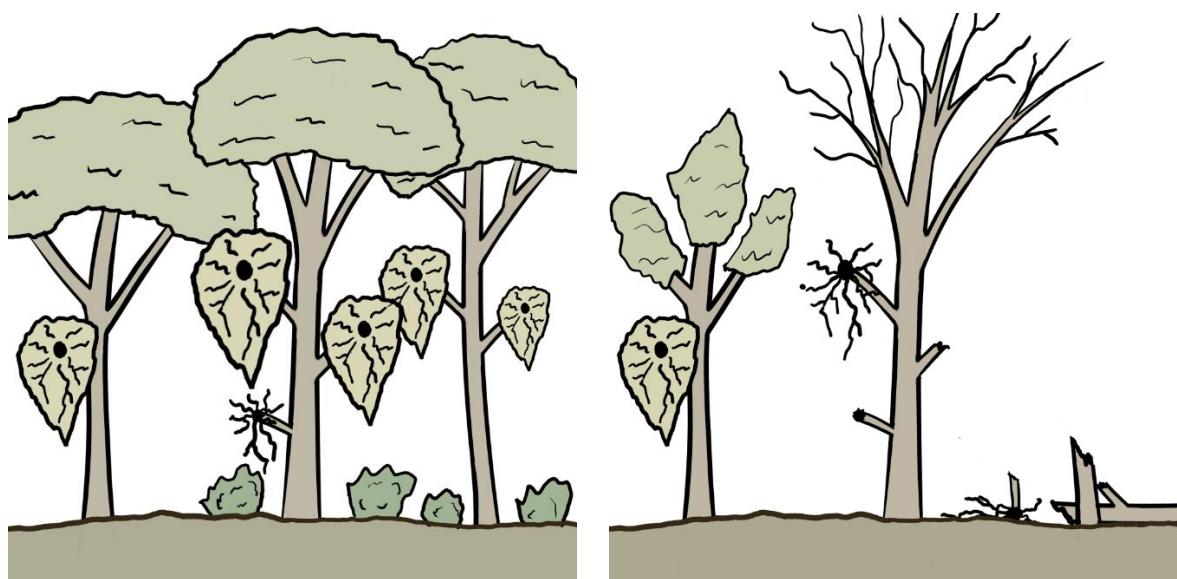


Figure 14. Simplified graphical representation of the survivor bias created following high severity fire. (a) depicts a forest structure pre-fire with 5 living mistletoes. (b) depicts the same forest structure post fire with 1 living mistletoe and 1 dead mistletoe. Note, two pre-fire mistletoes are indetectable due to tree fall, and 1 dead mistletoe is among the ground litter due to branch fall. This presents an observed survival rate of 50%, or 33% including the fallen mistletoe, deviating from the true survival rate of 20%. Additionally, (a) depicts a single pre-fire deceased mistletoe. The haustoral interface is still visible in (b) but has been excluded from the analysis.

12.37 hectares with an expected pre-fire count of 948 mistletoes. With 304 living mistletoes identified the corrected survival was 32.1% for low severity. Moderate severity represented 43.2 hectares with an expected pre-fire count of 3312 mistletoes. With 152 living mistletoes identified the corrected survival was 4.59% for moderate severity. High severity represented 26.0 hectares with an expected pre-fire count of 1996 mistletoes. With 7 living mistletoes identified the corrected survival was 0.351% for high severity. This represents a dramatic reduction in survival rate when compared to the uncorrected survival rate of 13.2% and predicted survival rate of 16.8%. The large discrepancy between corrected survival and predicted survival suggests that model 1 is ineffective at predicting the survival rate of pre-fire mistletoes. The corrected survival could be verified by a complementary study that designed for sampling the pre- and post-fire densities of living mistletoes. A distance sampling survey, calibrated to mistletoe detection probability, would provide a more comprehensive analysis of this relationship (Thomas et al. 2010).

The host fire health rating was chosen as a predictor variable to directly compare a remotely sensed model to a field observation model. Host fire health measures the damage sustained by an individual tree by its post-fire resprouting response. This is a useful indicator of post-fire tree health for the Eucalypt genera *Angophora*, *Corymbia*, and *Eucalyptus* which predominantly display epicormic, lignotuber, or combination resprouting responses to fire (Nicolle 2006). This is not an effective metric of tree health for obligate-seeding genera within the WNP, including: *Acacia* (Gordon, Price & Tasker 2017) and *Callitris* (Denham et al. 2016). As mistletoes are hemi-parasitic, they are affected by the host tree health. Studies have shown that mistletoes will die when the above ground portion of the host dies, even when the host survives through basal resprouting (Start 2015). I propose that once the host is damaged enough that branch death occurs mistletoe survival will be 0. Trunk resprouting, basal resprouting, or host death all include branch death. The thesis found that the observed survival rate of mistletoes was 63.1% on hosts with superficial or no fire damage. This reduces to 42.7% for trees with some degree of crown scorch where the terminal branches were not consumed. This suggests that mistletoes can survive some crown scorch and resulting foliage loss. This agrees with existing literature that showed *Amyema* mistletoes were capable of epicormic regrowth on the stem and haustorium after brief periods of burning (Kelly et al. 1997). This regrowth was present on mistletoes where the smaller stems (>7mm) were killed but not consumed (Kelly et al. 1997). A single living mistletoe was found on a trunk resprouting host giving an observed survival rate of 2.63%. Basal resprouting and deceased hosts both showed a survival rate of 0%. This confirms the hypothesis that mistletoe survival responds negatively to increasing host fire health rating. The proposal that branches death would result in mistletoe death was supported but not completely affirmed with one trunk resprouting survivor. That mistletoe was identified as *A. miquelii* on a *C. trachyphloia* in moderate severity. I propose that the survivor was on a larger trunk-like branch that was not killed in the fire, but further investigation would be required to draw conclusions.

The mechanisms by which mistletoe survival was overestimated for higher fire severities is likely to also apply to host fire health. The number of pre-fire mistletoes for trunk resprouting, basal resprouting, and deceased host trees is likely to be much larger than the number of observed post-fire mistletoes. This would not affect the survival of basal or deceased hosts but may suggest that the 2.63% survival for trunk resprout is superficially high.

From this relation, I propose that fire severity is an effective predictor of mistletoe survival for remotely sensed assessments following high severity fire. However, model 1 as presented contains a significant error sourced from the survivor bias and should not be used to predict mistletoe survival. Host fire health rating is a stronger predictor for mistletoe survival following high severity fire. However, as it is a field observation it is not effective for application to large-scale remote analysis for use in ecological management. The corrected survival presented closely agrees with field observations and existing literature. The transect design used for the thesis was not conducive to developing a fire severity abundance model due to transects regularly crossing multiple fire severities. Subsequent studies attempting to determine mistletoe survival should quantify the difference in abundance of mistletoes as a function of fire severity. A differenced post-fire abundance model would be effective for application in large-scale remote analysis in ecological management and future high severity fire events.

5.2 Additional Predictors for Mistletoe Survival

The effect of haustorium height on mistletoe survival was chosen to assess the prediction by Kelly et al. (1997) that low hanging mistletoes would be killed during low intensity fire. The hypothesis that mistletoe survival would respond positively to increasing survival was not statistically supported by this thesis. A weak relationship ($P < \alpha = 0.10$) was shown but did not meet the α (0.05) of this thesis. No relation between survival and height was observed when higher fire severity categories were excluded from the analysis to remove the effect of fire severities where the canopy was partially or fully immersed in fire (Gibson et al. 2020). The outcome of model 3b shows that even for low severity where only the grass, herb, and shrub layer are immersed in fire (Keeley 2009) the height of the mistletoe does not play an important factor in determining its survival. As larger trees were less likely to suffer topkill following the Wambelong fire (Denham et al. 2016), it suggests that the deaths of high canopy mistletoe occurred where the host branch survived.

The hypothesis that mistletoe survival would respond positively to increasing mistletoe size was supported by the thesis. This was chosen to assess the observation that small mistletoes suffer greater mortality than large mistletoes (Kelly et al. 1997). The frequency of mistletoe size was represented by a strong positive distribution skew that shows a high frequency of small mistletoes ($<= 1 \text{ m}^2$) and a small frequency for large mistletoes ($>= 5 \text{ m}^2$). The survey showed a strong correlation between size and survival. The largest survivor was on average 1.2 m^2 larger than the largest dead mistletoe. In addition, large mistletoes showed a 46.4% increase in observed survival when compared to small

mistletoes, or a 17.5% increase when compared to mid-range mistletoes. This relationship is attributed to the thicker bark on the branches and haustoria of larger mistletoes which more effectively protects the subcortical buds to enable resprouting after short periods of burning (Kelly et al. 1997). This relationship between stem width and survival has been well documented for larger trees (Moylan 2021; Trouvé et al. 2021) and appears to function similarly in mistletoes. As none of the species in the WNP have displayed resprouting capability after scorch (Start 2011, 2015) it is likely mistletoe size determines the survival of individuals not subject to direct flame immersion. It is important to note that the consumption of small diameter mistletoe branches in higher severity fire may account for some bias in the results. This bias is limited by the exclusion of haustoral interface from the dataset, meaning all recorded mistletoe had some degree of branch structure remaining. However, it is still likely that some deceased mistletoes had a larger pre-fire size.

The hypothesis that mistletoe survival would vary depending on host species was supported by this thesis. Three host species, *Callitris*, *E. blakelyi* and *E. crebra*, were identified with low survival rates that significantly deviated from the sample population average. *E. crebra* is a species that has been demonstrated to have a high vulnerability to fire with a significant increase in topkill when compared to other ‘ironbark’ Eucalypts (Nolan et al. 2020). This suggests that a high ratio of topkill following the fire contributed to the lowest observed survival of any host with a high sample population. *Callitris* are fire vulnerable, obligate-seeders that are predominantly killed at moderate and high severity (Denham et al. 2016). *Callitris* have been shown to escape fire when they are the dominant tree in low severity fire (Denham et al. 2016) due to the reduction in flammability caused by the tree ground litter (Cohn et al. 2011). This suggests that for *Callitris*, the host species may increase mistletoe survival in low severity through fire suppression but decrease survival in high severity due to a high host mortality rate. 21 *Callitris* were sampled in unburnt and low severity areas, while 23 were sampled in moderate to high. Despite this the observed survival is still low across all samples. I propose this may be a detectability issue for live *M. bidwillii* in healthy *Callitris* due to the dense host foliage and the high degree of mistletoe-host mimicry. The deceased *M. bidwillii* were easy to distinguish from the *Callitris* when no foliage was present due to a distinct broom like structure. No such significant bias was observed for *E. blakelyi* and *E. crebra* hosts.

The hypothesis that mistletoe survival would vary with host ecological community was supported by this thesis. Two ecological communities, C3: White Box - Ironbark - White Pine and C4b: Apple - Yellow Box - Red Gum, were observed with low survival rates that deviated significantly from the survey population. Both significant ecological communities contain at least host species that was identified to significantly decrease the survival rate of mistletoes. C3 contain *Callitris* and *E. crebra* as dominant species in the community. C4b contains *E. blakelyi* as a dominant species in the community. This suggests that host species and host ecological community represent a similar signal for the survival rate of mistletoes. As host species is a field observation it is ineffective for use in large-scale ecological

management. Host ecological community is remotely sensed metric that is effective for application to large-scale ecological management and post-fire events. However, for application on ecological communities not present in the WNP a ground truthing study would be required to determine the survival rate or abundance of mistletoes for each ecological community.

5.3 Implications for Mistletoe Management

This thesis found that fire severity had a dramatic effect on the survival of mistletoes with a large difference in abundance between lower severity and higher severity areas. This shows that a large continuous section of the Warrumbungle National Park has had the mistletoe population eliminated by the 2013 Wambelong fire. In the 9 years since the fire no degree of recovery was observed suggesting a multi-decal recovery period for mistletoes. This has serious implications for the avian population of the WNP that rely on mistletoes for food or habitat.

The findings of this thesis agree with the consensus that fire plays an important role in dictating the spatial distribution of mistletoes (Gosper & Prober 2020; Start 2015; Turner & Smith 2016). It is important for ecological management to understand the dynamics between mistletoe survival, persistence, and fire severity. Low severity fires have been shown to cause a considerable population loss for mistletoes, however they do persist at a landscape level through low severity fire and do not need to recolonise through edge recruitment. This suggests that frequent low severity burns may be beneficial to mistletoes populations to mediate the build-up of moderate to high density fuels and coarse woody debris that contribute to high severity fires. Mistletoe populations following low fire severity would continue to support frugivorous birds at a landscape level at a reduced carrying capacity. However, it is unlikely that frequent fires would affect the build-up of small, low-density fuels that contribute to flame height and canopy scorch.

Other important factors that determine mistletoe distribution include host specificity (Carnegie et al. 2009; Start 2011, 2013, 2015), water availability (Crates et al. 2022; Watson 2015), and the behavioural patterns of mistletoe dispersers (Ward & Paton 2007; Watson 2013; Watson & Rawsthorne 2013). Each of these factors interact with fire in some way. Host specificity has been observed to determine mistletoe interactions with fire (Start 2011). Mistletoes with low host specificity that parasitise a wide array of families and genera are associated with a greater ability to recolonise burnt areas (Start 2015). This characteristic is more present in *Lysiana* mistletoes (Start 2015) but has not been observed in any WNP mistletoes. High host specificity mistletoes commonly parasitise fire-safe hosts (Start 2015). Changes to water availability during droughts has been observed to cause significant mistletoe die-offs where the host persists. This is attributed to the mistletoes lack of water storage organ, inability to close stomata, and loss of water gradient (Crates et al. 2022; Watson 2015). As droughts are associated with promoting fire conditions (Sullivan et al. 2012) it can be expected that the compounding effects of drought and fire would severely threaten mistletoe populations.

Biodiversity and population size of frugivorous birds has been shown to decline following severe fire or drought (Stevens & Watson 2022). This decrease in populations following fire and drought has been shown for Mistletoebirds and Honeyeaters, which are both in serious decline in the WNP (Stevens & Watson 2022). The dispersal of mistletoe seeds has been observed as a positive feedback pattern that encourages the aggregation of mistletoes near pre-established infections (Rawsthorne et al. 2012; Ward & Paton 2007). The probability of the long distance dispersal (>500 m) of a mistletoe seed when consumed by a Mistletoebird is less than 3% (Ward & Paton 2007). This low probability is compounded by the low rate of successful establishment ranging from 3% (Watson 2022) to 6% (Forestry and Timber Bureau 1968) for Australian mistletoes which suggests that successful long distance dispersal is a rare event. It is likely that the reduction in mistletoe abundance observed in moderate and high severity areas would cause a response in the movement patterns of birds that rely on mistletoes for food or habitat, favouring unburnt and low severity areas with greater populations of mistletoes. This suggests that the positive feedback of restricted mistletoe seed shadow would also apply to fire severity, favouring establishing mistletoes in high abundance, low severity areas. This means that the predominant mechanism by which mistletoes re-establish is a gradual edge recruitment into higher severity areas with rare events of long-distance dispersal.

The WNP was predominantly affected by moderate to high severity fire. The higher severity classes dominated 72% of the parks area (Tulau et al. 2019; Yang et al. 2018), spatially representing much of the northern, central, and eastern extents of the park. This region contained a live mistletoe abundance ranging between 3.52/ha to 0.269/ha, reduced from expected 53.2/ha prior to the fire. It can be expected that in much of the high severity area, the live mistletoe abundance is 0/ha given that all identified living mistletoe were within 5m of a lower severity class. This suggests that mistletoe dispersers may occasionally visit surviving mistletoes in moderate severity and bordering high severity. From there, random seed dispersal would promote gradual edge recruitment into the fire affected area. The rate at which mistletoes re-establish through edge recruitment has not been documented. This information will be useful for informing fire regime models to determine the minimum fire interval to maintain mistletoe population. However, studies have shown that the process can take in excess of 35 years before mistletoes will re-establish after fire, showing that they are a post-fire obligate coloniser (Gosper & Prober 2020). The study by Gosper and Prober (2020) also showed that some mistletoe species are true fire vulnerable plants, demonstrated through *L. casuarinae*, which was absent from fire plots up to 200 years after fire. This partially disagrees with similar studies that found *L. casuarinae* has two distinct forms, one of which can be considered a rapid re-coloniser and one can be considered extremely host specific (Start 2015).

The WNP may provide an important example for the process of edge recruitment for further studies. This is because a large section in the middle of the park was protected from the high severity fire. This includes the Central Valley and Wambelong Creek heading westwards from the Central Valley. This

area is isolated by higher severity areas that bound its northern, eastern, and southern extent. The central protected area had a much higher observed survival rate of mistletoes than the surrounding area. I attribute this to the fire origin along Wambelong creek, suggesting the fire had not developed a high intensity when it burned through the area. The Central Valley is a heavily cleared environment full of exotic weeds that would have been characterized by low grassfire. This means this isolated, protected mistletoe community may demonstrate edge recruitment from within the higher severity area. This may be important for establishing post-fire colonisation patterns in subsequent large scale, high severity fires. Despite the lack of colonisation identified during this thesis, the WNP provides an excellent candidate for future studies documenting the rate and patterns of mistletoe colonisation following high severity fires.

The effect of mistletoe population and distribution reduction in the WNP has a negative connotation for the avian biodiversity of the park. Mistletoes, as a keystone species (Watson 2001), have been shown to have a significant effect on the biodiversity of frugivorous (Crates et al. 2022; Watson & Herring 2012) and insectivorous birds (Mellado et al. 2019). As the population of mistletoes have been dramatically reduced in a large portion of the park it is expected to have a significant impact on the avian population. This is supported by Stevens and Watson (2022) who have demonstrated a drastic decline for 15 bird species in the WNP resulting from the 2013 Wambelong fire or a combination of the 2013 fire and the 2017-2019 drought. The Department of Planning and Environment has shown interest in the effect of the Wambelong fire on the Regent Honeyeater. The study by Stevens and Watson (2022) did not address the Regent Honeyeater individually but did show an abundance reduction for the Honeyeater group. It has been shown that the Regent Honeyeater relies on mistletoe for nest substrate (Oliver 2000; Thomas 2009). Thus, I propose that the increased competition for habitat following the fire will have a significant impact on the critically endangered species.

As the fire may have adversely affected a critically endangered species it may be advantageous for conservation efforts to trial a manual re-establishment program for mistletoes within the WNP. Manual establishment has been proven effective with a recent successful reintroduction program in Melbourne VIC (Watson 2022). I propose the most effective method would be to establish mistletoes along lines through the higher severity area to create a colony passageway that provides food and habitat for frugivorous birds. This could maximise the speed at which edge recruitment occurs, dividing a large higher severity area into smaller areas. This helps to maximise the edge to area ratio for edge recruitment. However, as mistletoes are an aerial habit plant, it may not be practical to create lines through the forest. This is due to access issues required for machinery such as cherry pickers that can access tree canopies to inoculate hosts with mistletoes. It may be more practical to seed mistletoes along existing fire access trails through the high severity area. It will also be important to protect trees against arboreal marsupials which graze on mistletoes and lead to high rates of juvenile mortality (Norton & Reid 1997; Sessions & Kelly 2001; Watson 2022). For the Melbourne establishment project this was

done through the instillation of possum collars on the host tree (Watson 2022). An alternative to line-based reintroduction would be plot based reintroduction. The WNP has many fenced biodiversity plots that prevent animal access. Establishing mistletoes in these plots in higher severity areas of the park would protect the juvenile mistletoes from vertebrate herbivory where the canopy structure does not mesh with surrounding forest to allow cross tree travel. It is likely that these sites would need to be within the 500-meter of each other to encourage visitation within the standard flight pattern of a Mistletoebird (Rawsthorne et al. 2012; Ward & Paton 2007), to ensure that sites are frequented by dispersers. It is not known if isolated sites with strong mistletoe populations will be visited if isolated.

5.4 Limitations

The accuracy and precision of this thesis is limited for mistletoe number, height, and size. This is due to the visual observation sampling method and lack of calibration study. The visual observation suggests that accuracy would reduce the farther the observer and mistletoe are. It was not practical within the constraints of the thesis to use more precise sampling techniques that would require accessing mistletoes, which were found to grow at heights up to 40m above the ground. This would require specialist training and equipment for accessing heights safely and reduce survey speeds. For future surveys calibration studies should be performed. A calibration study for mistletoe number would require walking a transect to identify the observed mistletoe number, before repeating the transect several times to determine the true mistletoe number. A calibration study for height and size would require comparing the estimated size from a ground observer to the known sizes of individuals at different heights. This could be used to determine an accuracy and precision value for the visual survey.

As the thesis assessed mistletoe height and size using the largest individual for each host, they have a different survey population to severity and host fire health rating. This issue was also present for host species and ecological community, which used reduced datasets to prevent small sample populations from invalidating results. This prevents the creation of a combination model through generalized linear mixed modelling. A combination model would account for all variables and may increase the degree of variance explained compared to the low goodness-of-fit models presented by this thesis. A change in approach to methodology would be required. Either a) only sampling 1 mistletoe from each host tree at random, or b) sampling all identified mistletoes for each host tree.

As mentioned in **section 5.1** there is significant survivor bias present in the design of this survey. This can be solved by changing the approach of future surveys to look at mistletoe abundance rather than survival. This was a flaw with the methodology that was not identified until after the data collection. As the effects of high severity fire on dead mistletoes may considerably change the results in favour of survivors, I recommend that future studies instead focus on the live mistletoe abundance compared to the expected pre-fire abundance. This also prevents the bias caused by the inability to distinguish haustoral interface of mistletoes that died before or after the fire.

A final issue exists with the methodology presented in discerning colonising mistletoes. Juvenile mistletoes are small and may take up to two years to develop foliage (Watson 2019), thus suffer from detectability issues from a ground survey. Additionally, any colonising mistletoe sufficiently mature enough to develop dense foliage would be indistinguishable from a fire survivor. No literature provides the rate of growth for Australian mistletoes so the maximum size of recolonisers is not known. Similarly, it was observed in this thesis that low canopy mistletoes were visibly smaller than higher canopy mistletoes. This suggests that mistletoes with more access to light resources have a greater maximum size but may also suggest a bias due to a minimum detectable size at great heights. Further research is required to discern these effects.

5.5 Conclusions

The effects of fire on mistletoes in Australia is a poorly documented and fragmentary field of literature. The literature assessing mistletoes fire dynamics is predominantly studies using prescribed fire as an ecological control for mistletoe infection (e.g. Kelly et al. 1997), or assessing mistletoe distribution long after fires (e.g. Gosper & Prober 2020; Start 2015). With literature increasingly supporting the concept of mistletoes as a keystone species with a particular importance for avian biodiversity (Napier et al. 2014; Těšitel et al. 2020; Watson 2001; Watson & Herring 2012), it has become important to understand the dynamics of mistletoes, a fire vulnerable obligate coloniser, with regards to wildfire. This relationship is important for informing the ecological management of mistletoes to predict effects on mistletoe reliant species like the Regent Honeyeater.

This thesis assessed the effect of the 2013 Wambelong fire on the mistletoe population of the Warrumbungle National Park to determine the effect of fire severity on the survival of mistletoes. The thesis concluded that increasing fire severity adversely affects mistletoes with high severity fire nearly eliminating all mistletoes. The thesis also found that mistletoe size and host species significantly influenced mistletoe survival. Contrary to the hypothesis, mistletoe height above ground level did not significantly increase the survival rate of mistletoes in the fire. The field metrics of host fire health rating and host ecological community were both stronger predictors of mistletoe survival than their remotely sensed counterparts, fire severity and host ecological community. However, both remotely sensed metrics were significant predictors for determining mistletoe survival. Despite this, the model presented for fire severity is ineffective for later use due to a large survivor bias created from measuring survival by the observed survival rate of mistletoes, rather than abundance of living mistletoes for each fire severity.

The thesis found that the large moderate to high severity area of the WNP was dominated by critically low rates of mistletoe survival. This region had a protected, isolated lower severity area containing the heavily cleared Central Valley and Wambelong Creek which had a relatively high mistletoe survival rate. The southern extent of the park was characterised by lower fire severity with moderate mistletoe

survival rates. This suggests that mistletoes can colonise the moderate to high severity area through edge recruitment from an external and internal population of mistletoes. However, studies into mistletoe colonisation in Western Australia suggests that this process may take up to 35 years before noticeable colonisation happens and up to 200 years before populations recover fully (Gosper & Prober 2020). Fire plays a crucial role in the distribution of mistletoes directly by causing premature mortality, and indirectly by changing the seed rain created by mistletoe dispersing species. Further research into the survival rate of mistletoes in high severity fire should focus on the abundance of living mistletoes rather than percentage of surviving mistletoes. This would allow a stronger fire severity model to be designed for application in future fire events. This will become increasingly important as the frequency and severity of large fires changes with the warming climate. Additionally, determining the recolonisation patterns of mistletoes following fire will be important for the management of mistletoe dependent species. There are several factors that can be assessed in this relationship, including the rate and distance of edge recruitment from surviving mistletoe colonies. Literature on mistletoe dispersal suggests that long distance seed dispersal occurs infrequently (Ward & Paton 2007; Watson & Rawsthorne 2013) and successful establishment rates are low (Forestry and Timber Bureau 1968; Watson 2022), suggesting that successful long distance seed dispersal is a rare event. Critically, these studies do not assess if long distance seed dispersal occurs into areas recently affected by high severity fire, as the lack of mistletoes may dissuade mistletoe dispersers from travelling into the area.

This thesis has shown that mistletoes are vulnerable to changes in the frequency and severity of fire regimes with changing temperature and climate from anthropogenic climate change. As an obligate post coloniser, mistletoes have no ability to survive high severity fire events and must rely on colonisation from lower severity refugia. An event like the Wambelong fire can seriously disrupt mistletoe populations over a large area and as a result, reduce the carrying capacity of frugivores in the environment with a potential multi-decadal recovery time. The Wambelong fire affected 55000 hectares of land, which was surpassed in 2019 by the Gospers Mountain megafire which burned over 500000 hectares of land as part of a clusters of fires that collectively burned over 1 million hectares in the Blue Mountains and surrounding region (Costello 2020). The implications of this study suggest that a fire of that size and severity would eliminate mistletoes on a massive regional scale where edge recruitment may be insufficient for mistletoes to recover effectively before the next major fire. Because of this it may become important to understand the dynamics of mistletoes persistence across multiple fire regimes to determine the minimum period between high severity fires that mistletoes require to successfully recolonise and persist on a landscape level.

Appendix A: Reference List

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Appendix B: List of Species

B1: Plant Species List

Family	Scientific Name	Common Name
Boraginaceae	<i>Echium plantagineum</i>	Patterson's Curse
Casuarinaceae	<i>Casuarina cunninghamiana</i>	River She-oak
Cupressaceae	<i>Callitris endlicheri</i>	White Cypress Pine
	<i>Callitris glauophylla</i>	Black Cypress Pine
Fabaceae	<i>Acacia cheelii</i>	Motherumbah
	<i>Acacia deanei</i>	Deane's Wattle
	<i>Acacia homalophylla</i>	Yarran
	<i>Acacia tetragonophylla</i>	Dead Finish
Loranthaceae	<i>Atkinsonia ligustrina</i>	Atkinsonia
	<i>Amyema bifucata</i>	Forked Mistletoe
	<i>Amyema cambagei</i>	Needle-leaf Mistletoe
	<i>Amyema linophylla</i>	Buloke Mistletoe
	<i>Amyema miquelii</i>	Box Mistletoe
	<i>Amyema miraculosa</i>	Fleshy Mistletoe
	<i>Amyema pendula</i>	Drooping Mistletoe
	<i>Amyema preissii</i>	Wireleaf Mistletoe
	<i>Amyema quandang</i>	Grey Mistletoe
	<i>Dendrophthoe glabrescens</i>	Smooth Mistletoe
	<i>Gaiadendron punctatum</i>	Gaiadendron
	<i>Lysiana exocarpi</i>	Harlequin Mistletoe
	<i>Muellerina bidwillii</i>	Callitris Mistletoe
	<i>Muellerina eucalyptoides</i>	Creeping Mistletoe
	<i>Nuytsia floribunda</i>	Western Australian Christmas Tree
	<i>Psittacanthus ramiflorus</i>	Parrot Flower Mistletoe
	<i>Tristerix aphyllus</i>	Chilean Cactus Mistletoe
Malvaceae	<i>Brachychiton populneus</i>	Kurrajong
Myrtaceae	<i>Angophora floribunda</i>	Rough-barked Apple
	<i>Corymbia trachyphloia</i>	Brown Bloodwood
	<i>Corymbia dolichocarpa</i>	
	<i>Eucalyptus albens</i>	White Box
	<i>Eucalyptus blakelyi</i>	Blakely's Red Gum
	<i>Eucalyptus crebra</i>	Narrow-leaved Ironbark
	<i>Eucalyptus dealbata</i>	Tumbledown Red Gum
	<i>Eucalyptus macrohyncha</i>	Red Stringybark
	<i>Eucalyptus melliodora</i>	Yellow Box
	<i>Eucalyptus racemosa</i> subsp. <i>rossii</i>	Inland Scribbly Gum
Poaceae	<i>Microlaena stipoides</i>	Weeping Grass
	<i>Austrostipa scabra</i>	Rough Spear Grass
	<i>Austrostipa verticillata</i>	Slender Bamboo Grass
Santalaceae	<i>Santalum acuminatum</i>	Desert Quandong
Verbenaceae	<i>Verbena bonariensis</i>	Purple-top Vervian
Viscaceae	<i>Notothixos cornifolius</i>	Kurrajong Mistletoe
	<i>Viscum album</i>	European Mistletoe

B2: Animal Species List

Family	Scientific Name	Common Name
Campephagidae	<i>Coracina novaehollandiae</i>	Black-faced Cuckoo-shrike
Columbidae	<i>Macropygia phasianella</i>	Brown Cuckoo-dove
	<i>Ptilinopus regina</i>	Rose-crowned Fruit-dove
Dicaeidae	<i>Dicaeum hirundinaceum</i>	Mistletoebird
Meliphagidae	<i>Acanthagenys rufogularis</i>	Spiney-cheeked Honeyeater
	<i>Anthochaera carunculata</i>	Red Wattlebird
	<i>Conopophila whitei</i>	Grey Honeyeater
	<i>Granitiella picta</i>	Painted Honeyeater
	<i>Lichenostomus fuscus</i>	Fuscous Honeyeater
	<i>Lichenostomus virescens</i>	Singing Honeyeater
	<i>Manorina flavigula</i>	Yellow-throated Miner
	<i>Meliphaga lewinii</i>	Lewin's Honeyeater
	<i>Oriolus sagittatus</i>	Olive-backed Oriole
Sturnidae	<i>Aplonis metallica</i>	Metallic Starling
Zosteropidae	<i>Zosterops lateralis</i>	Silvereye