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The Effects of Myrtle Rust on Post-Fire Regeneration of Myrtaceae in Australia

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ABSTRACT

Fire is an important factor influencing the evolution, structure and composition of Australia's native vegetation. Australia's many fire-adapted species regenerate en masse after fire, with a proliferation of new epicormic shoots and seedlings. Given *Austropuccinia psidii* (myrtle rust) mainly infects new growth, post-fire emergence of new epicormic shoots and seedlings is ideal for the development of the disease, leading to further loss of plants along with subsequent increase of fungal inoculum in the region. Extreme fire events across New South Wales and Queensland in 2019–2020 and subsequent vegetation regeneration across a wide area provided ideal conditions for disease epidemics. Surveys for myrtle rust were conducted across rainforest, coastal heath and woodland environments from south-eastern NSW to south-east Queensland 6–12 months post-fire. Myrtle rust was identified in all regions and ecosystems surveyed apart from areas in south-eastern NSW. Of the 73 Myrtaceae species surveyed in areas other than southern NSW, 44 were found with myrtle rust symptoms, ranging from small spots and limited damage to severe blighting, dieback and death of resprouting trees and seedlings. Monitoring plots were established for some of the more susceptible species, with monthly assessments conducted to determine impact levels and decline rates. The most severely impacted species were *Rhodamnia rubescens* and *Uromyrtus australis*, with infections of resprouts causing dieback. Infection of *Melaleuca quinquenervia* and *M. nodosa* resprouts and seedlings impeded recovery of populations, causing seedling and tree deaths and reducing flower set and subsequent seed production.

1 | Introduction

The Black Summer (2019/2020) wildfires were unprecedented in extent and severity (Auld 2020; Legge et al. 2021) burning over 24 million ha in eastern Australia (Christoff 2023), including 8.34 million ha of forest (Davey and Sarre 2020). Seventeen major native vegetation groups within 11 Australian bioregions were severely burned, including globally significant rainforests and eucalypt forests and woodlands (Godfree et al. 2021). In New South Wales (NSW), 5.3 million ha (6.7% of the state)

were fire-affected, including 2.7 million ha in National Parks (37% of the state's National Park estate) (Forest fire data—DAFF; agriculture.gov.au). Coastal and near-coastal bioregions were some of the most fire-affected vegetation types (Godfree et al. 2021).

Fire occurs over much of the Australian landscape, in most vegetation types (Davey and Sarre 2021), and is an important factor influencing plant diversity and vegetation community structure (Gill 1999). This includes rainforests, but there are a

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wide variety of fire regimes that occur across these ecosystems (Gill et al. 1981). Post-fire resprouting and seedling recruitment are key traits influencing plant community composition and function (Baker et al. 2021). Auld (2020) emphasises that fires do not necessarily destroy bushland, as Australian flora have strategies to survive fires and recover.

Following fire, conditions favour plant recovery through increased nutrient availability, improved light conditions and space promoting growth (Auld 2020). Species that regenerate via resprouting have dormant buds beneath their bark that survive the heat of a fire, or dormant buds, or underground organs, protected from the heat (Auld 2020). Fire-affected plants may also recruit through seeds stored in woody fruits or in soil seed banks, whereby fire stimulates germination. Sufficient post-fire rainfall triggers mass seedling germination. However, the recently introduced rust fungus *Austropuccinia psidii* (myrtle rust) is a new threat to the post-fire recovery process (Godfree et al. 2021; Keighery et al. 2023).

Austropuccinia psidii is native to South America and was detected in Australia for the first time in 2010 on the central coast of NSW (Carnegie et al. 2010). Spreading rapidly, it is now found on the east coast from Tasmania to Bamaga at the tip of Cape York Peninsula, the Tiwi Islands and Darwin in the Northern Territory (Carnegie and Pegg 2018; Makinson 2019), and northern Western Australia (The Department of Primary Industries and Regional Development 2022).

Austropuccinia psidii affects plants in the Myrtaceae family. The current host range in Australia exceeds 380 species from 58 genera (Soewarto et al. 2019) occurring across a range of native ecosystems: coastal heath, coastal and river wetlands, sand island ecosystems, and littoral, montane, subtropical and tropical rainforests (Pegg, Giblin, et al. 2014). In the short time that *A. psidii* has been established in Australia, significant plant damage and mortality have occurred, severely affecting key species in natural ecosystems (Carnegie et al. 2016; Pegg et al. 2017; Fensham et al. 2020, 2021). Impacts on plant communities have become more apparent, with tree mortality causing species composition changes (Pegg et al. 2017). Myrtle rust is now recognised legislatively as a Key Threatening Process and many species have been listed as Critically Endangered in Queensland, NSW, and under the Commonwealth's Environment Protection and Biodiversity Conservation Act 1999.

The impact of *A. psidii* infection on regeneration of species post-fire has been reported previously (Pegg et al. 2020), although myrtle rust impacts are not restricted to areas or species that have been affected by a disturbance event (Carnegie et al. 2016; Fensham et al. 2021; Pegg, Giblin, et al. 2014). This was an opportunistic study, with the aim of gathering information on a broad range of Myrtaceae species across a wide geographic area in fire-affected ecosystems in NSW (Northern Rivers, Central and South Coast) and South East Queensland. Using monitoring plots, we also examined the effect of repeated infection on recovery and survival of *Eucalyptus pilularis*, *Melaleuca quinquenervia* and *M. nodosa*.

2 | Methods

2.1 | Surveys

To assess the impact of myrtle rust on post-fire regeneration of a broad range of Myrtaceae across multiple ecosystems in eastern Australia, we conducted one-off surveys from southern NSW to South East Queensland, with all assessments completed during the period from May to October 2020 (Figure 1, Table 1). Site selection was based on areas impacted by fire using maps (State Government of NSW and NSW Department of Climate Change, Energy, the Environment and Water 2020), flora composition and local land manager information enabling us to target sites where Myrtaceae were present and abundant. This was not intended to be a detailed survey but an opportunistic study to gather information on the impact of myrtle rust on post-fire recovery from a wide range of sites and species. Due to differing species composition at sites, variability in fire severity, and constraints on access due to terrain and/or weather, there was variability in the surveillance methodology relating to the number of plants surveyed and time spent surveying per site. Where possible, 50 m transects were used, and all Myrtaceae occurring within a metre of the transect were assessed for disease levels. "Walkthrough" surveys, approximately 50 m transects from a road or track edge, were also conducted at some sites, with any Myrtaceae plants present assessed. Each Myrtaceae plant was assessed for: (1) presence/absence of *A. psidii* infection, and (2) severity of myrtle rust infection (area of infected new growth—foliage and juvenile stems—with rust sori) using a disease infection ranking of low, moderate, high and severe (Table 1), adapted from Pegg et al. (2014).

2.2 | Disease Impact Monitoring Plots

To gather more detailed information on individual species, monitoring plots were established in selected sites to assess the effects of repeated *A. psidii* infection on post-fire regeneration. Fifty trees per plot were chosen randomly and labelled with flagging tape. Assessment frequency varied due to Covid-19 restrictions and flooding affecting access, but where possible recordings were made monthly. Plots were established in NSW northern rivers (Yarrungully Nature Reserve, Bundjalung National Park) and sites on the Central Coast, NSW. Sites were selected based on the abundance of key hosts; species assessed were *E. pilularis*, *M. quinquenervia* and *M. nodosa*.

Disease assessment methods were adapted from previous studies (Pegg, Giblin, et al. 2014; Pegg et al. 2017, 2020; Carnegie et al. 2016). Each tagged tree was assessed for:

- Presence or absence of new growth (susceptible to *A. psidii* infection).
- Disease incidence: Percentage susceptible new growth with *A. psidii* symptoms.
- Disease severity: severity of *A. psidii* infection on affected growth: low; moderate; high; severe.

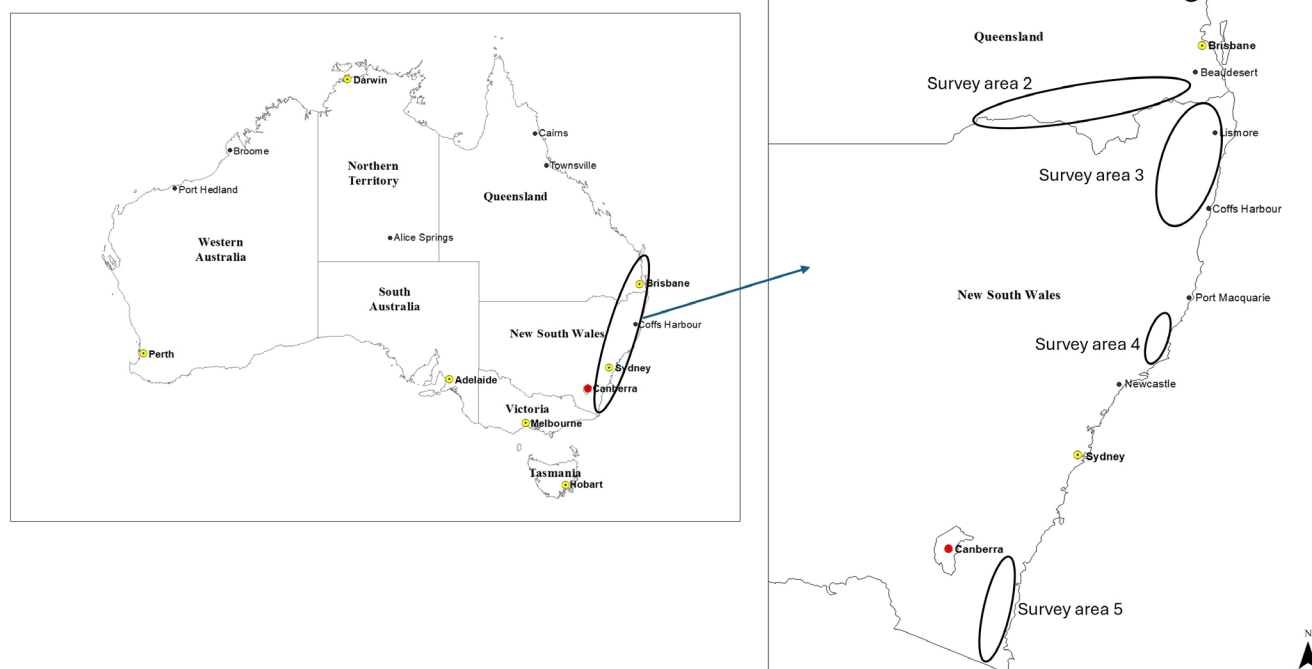


FIGURE 1 | Map showing areas surveyed across South East Queensland, northern, central and southern New South Wales for myrtle rust impacts on wildfire affected Myrtaceae. Surveys were conducted from May to October 2020.

- Tip dieback on reshoots (Percentage of reshoots with dieback).
- Reshoot death (Percentage reshoots per tree killed by myrtle rust).
- Flowering: 0–4 rating: 0 = no flowers; 1 (low) = 1%–25%, 2 (moderate) = 26%–50%, 3 (abundant) = 51%–75%, 4 (very abundant) = 76%–100% of branches with flowers or buds.

3 | Results

3.1 | Surveys

Twenty-two areas were surveyed, from the southern NSW border to Coolool National Park in South East Queensland (Table 1; Figure 1). Vegetation types assessed were coastal heath, paperbark wetlands, coastal and inland woodland habitats, *Eucalyptus* forests and subtropical rainforest in the Gondwana Rainforests of Australia World Heritage Area, and temperate coastal woodlands. Fire intensity levels varied across and within sites. Due to Covid-19 restrictions, areas in eastern Victoria were unable to be surveyed as initially planned. Surveys of areas in south-eastern NSW (Ulladulla to the Victorian border) were conducted in October 2020, with no evidence of myrtle rust identified (data not presented), although the disease is known from this region (Carnegie et al. 2016; Berthon et al. 2018). Assessments for rust in this region of NSW were conducted on *Acmena smithii*, *Backhousia myrtifolia*, *Eucalyptus elata*, *Kunzea ambigua*, *Leptospermum polygalifolium*, *L. trinervium*, *Melaleuca ericifolia*, *M. linariifolia* and *Tristaniopsis laurina*. A return survey to

southern NSW was not possible due to Covid-19 travel restrictions being imposed.

For areas surveyed other than south-eastern NSW, seventy-three species across 24 genera of Myrtaceae were surveyed. Forty-four species (60.27%) had evidence of myrtle rust infection and impact (Table 1), ranging from small spots and limited damage to severe blighting, dieback and death of resprouting trees and seedlings because of repeated infection. An example of the symptoms observed is provided in Figure 2.

Populations of *M. quinquenervia*, *M. nodosa* and *Rhodamnia rubescens* (Figure 2) were severely impacted by *A. psidii* in fire-affected areas where they were present. For coastal NSW populations of *E. pilularis*, seedling and reshoots had varying levels of severity of infection recorded. Populations of *Uromyrtus australe*, a species with a restricted native range, were identified with *A. psidii* infection and dieback on reshoots. Regenerating *B. sciadophora* was found with moderate levels of infection across fire-affected habitats in northeastern NSW. There is currently very little information on the impact of *A. psidii* on this species across its native range.

3.1.1 | Disease Impact Monitoring Plots

While *R. rubescens* recovery was found to be severely affected by myrtle rust, the status of this species has already been studied in detail (Carnegie et al. 2016; Fensham et al. 2021). Plots were established to look at impacts on *E. pilularis* but were discontinued after a short period. While reshoots were severely infected,

TABLE 1 | Survey locations, fire severity, plant species and type of regeneration (State Government of NSW and NSW Department of Climate Change, Energy, the Environment and Water 2020) assessed for myrtle rust (*Austropuccinia psidii*) symptoms and infection severity. Regeneration type assessed R = reshoots; S = seedling. Infection levels L = low; M = moderate; H = high; S = severe.

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
Queensland	Great Sandy National Park/Transect surveys	Coastal heath, paperbark wetland and woodland, Littoral Rainforest	Low-High	<i>Aemena smithii</i>	R	Yes	14.8 (n = 27)	L-S
				<i>Austromyrtus dulcis</i>	R	Yes	57.2 (n = 55)	L
				<i>Backhousia myrtifolia</i>	R	Yes	25.71 (n = 105)	L-H
				<i>Baeckea frutescens</i>	R	No	0 (n = 126)	
				<i>Corymbia intermedia</i>	R	No	0 (n = 20)	
				<i>Corymbia tessellaris</i>	R	No	0 (n = 1)	
				<i>Eucalyptus pilularis</i>	S/R	No	0 (n = 23)	
				<i>Eucalyptus racemosa</i>	R	No	0 (n = 6)	
				<i>Eucalyptus robusta</i>	R	No	0 (n = 7)	
				<i>Homoranthus virgatus</i>	R	Yes	20 (n = 25)	L-H
	Noosa National Park/Transects surveys	Coastal heath, paperbark wetland	Moderate-High	<i>Leptospermum liversidgei</i>	R	Yes	8.1 (n = 37)	L-M
				<i>Leptospermum trinervium</i>	R	No	0 (n = 5)	
				<i>Lophostemon confertus</i>	S/R	No	0 (n = 27)	
				<i>Melaleuca quinquenervia</i>	R	Yes	10.29 (n = 68)	L-S
				<i>Rhodannia acuminata</i>	R	No	0 (n = 16)	
				<i>Syzygium leuhmannii</i>	R	No	0 (n = 12)	
				<i>Syzygium oleosum</i>	R	Yes	42.86 (n = 7)	L-H
				<i>Austromyrtus dulcis</i>	R	No	0 (n = 14)	
				<i>Baeckea frutescens</i>	R	No	0 (n = 61)	
				<i>Leptospermum liversidgei</i>	R	Yes	29.73 (n = 37)	L-M
				<i>Leptospermum polygalifolium</i>	R	Yes	30.36 (n = 56)	L-M
				<i>Leptospermum semibaccatum</i>	R	No	0 (n = 3)	
				<i>Melaleuca pachyphylla</i>	R	Yes	4.5 (n = 221)	L
				<i>Melaleuca quinquenervia</i>	R	Yes	17.65 (n = 17)	L-S
				<i>Melaleuca thymifolia</i>	R	No	0 (n = 54)	

(Continues)

TABLE 1 | (Continued)

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
Survey Area 2								
Lamington National Park/ Walkthrough surveys		Subtropical Rainforest	Low–High	<i>Acmena ingens</i>	S/R	Yes	2 (<i>n</i> = 40)	L
				<i>Acmena smithii</i>	R	No	0 (<i>n</i> = 2)	
				<i>Backhousia myrtifolia</i>	R	No	0 (<i>n</i> = 1)	
				<i>Eucalyptus acmenoides</i>	R	No	0 (<i>n</i> = 18)	
				<i>Eucalyptus microcorys</i>	R	No	0 (<i>n</i> = 4)	
				<i>Gossia acmenoides</i>	R	No	0 (<i>n</i> = 6)	
				<i>Gossia bidwillii</i>	R	No	0 (<i>n</i> = 3)	
				<i>Lophostemon confertus</i>	S/R	No	0 (<i>n</i> = 1000)	
				<i>Ptilidostigma glabrum</i>	R	Yes	14 (<i>n</i> = 7)	L–M
				<i>Rhodamnia rubescens</i>	R	Yes	94 (<i>n</i> = 18 + 2 dead)	L–S
				<i>Syzygium australe</i>	R	No	0 (<i>n</i> = 17)	
				<i>Syzygium francisii</i>	S/R	No	0 (<i>n</i> = 24)	
				<i>Syzygium oleosum</i>	R	No	10 (<i>n</i> = 10)	L–M

(Continues)

TABLE 1 | (Continued)

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
Mt Barney National Park/ Walkthrough surveys		Subtropical Rainforest	Low–Moderate	<i>Backhousia myrtifolia</i>	R	Yes	0 (<i>n</i> = 9) dieback only	L
				<i>Eucalyptus acmenoides</i>	S/R	No	0 (<i>n</i> = 3)	
				<i>Eucalyptus grandis</i>	S	No	0 (<i>n</i> = 17)	
				<i>Eucalyptus microcorys</i>	R	No	0 (<i>n</i> = 3)	
				<i>Eucalyptus propinqua</i>	R	No	0 (<i>n</i> = 1)	
				<i>Gossia acmenoides</i>	R	No	0 (<i>n</i> = 2)	
				<i>Lophostemon confertus</i>	S/R	No	0 (<i>n</i> = 16)	
				<i>Rhodamnia rubescens</i>	R	Yes	89 (<i>n</i> = 9 + 1 dead)	L–S
				<i>Rhodomyrtus psidioides</i>	R	Yes	100 (<i>n</i> = 1)	M–H
				<i>Syncarpia glomulifera</i>	R	No	0 (<i>n</i> = 8)	
				<i>Syzygium australe</i>	R	No	50 (<i>n</i> = 2)	L–S
				<i>Syzygium oleosum</i>	R	No	0 (<i>n</i> = 6)	
				<i>Lophostemon confertus</i>	S/R	No	0 (<i>n</i> = 14)	
				<i>Backhousia myrtifolia</i>	R	No	0 (<i>n</i> = 4)	
				<i>Eucalyptus acmenoides</i>	S/R	No	0 (<i>n</i> = 2)	
				<i>Eucalyptus microcorys</i>	S/R	No	0 (<i>n</i> = 2)	
				<i>Eucalyptus grandis</i>	S	No	0 (<i>n</i> = 10)	

(Continues)

TABLE 1 | (Continued)

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
New South Wales	Main Range National Park/ Walkthrough surveys	Subtropical Rainforest	Low–High	<i>Acmena ingens</i>	S/R	No	0 (<i>n</i> = 17)	
				<i>Acmena smithii</i>	R	No	0 (<i>n</i> = 15)	
				<i>Angophora subvelutina</i>	R	No	0 (<i>n</i> = 6)	
				<i>Corymbia intermedia</i>	R	No	0 (<i>n</i> = 1)	
				<i>Eucalyptus acmenoides</i>	S/R	No	0 (<i>n</i> = 8)	
				<i>Eucalyptus campanulata</i>	R	No	0 (<i>n</i> = 2)	
				<i>Eucalyptus dunnii</i>	R	No	0 (<i>n</i> = 1)	
				<i>Eucalyptus microcorys</i>	S/R	No	0 (<i>n</i> = 6)	
				<i>Eucalyptus punctata</i>	R	No	0 (<i>n</i> = 4)	
				<i>Eucalyptus saligna</i>	R	No	0 (<i>n</i> = 2)	
				<i>Eucalyptus tereticornis</i> subsp. <i>basaltica</i>	R	No	0 (<i>n</i> = 8)	
				<i>Leptospermum variabile</i>	S/R	No	0 (<i>n</i> = 3)	
				<i>Lophostemon confertus</i>	S/R	No	0 (<i>n</i> = 26)	
				<i>Rhodamnia rubescens</i>	R	Yes	66 (<i>n</i> = 35 + 14 dead)	L–S
				<i>Rhodamnia whiteana</i>	R	Yes	60 (<i>n</i> = 5 + 1 dead)	L
				<i>Syzygium australe</i>	R	Yes	31 (<i>n</i> = 13)	L
				Survey Area 3				

(Continues)

TABLE 1 | (Continued)

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
Northern Rivers	Nightcap Range National Park/Walkthrough surveys	Subtropical Rainforest	Low–High	<i>Acmena smithii</i>	R	No	0 (<i>n</i> = 9)	
				<i>Archirhodomyrtus beckeri</i>	R	Yes	41 (<i>n</i> = 56)	L
				<i>Decaspermum humile</i>	R	Yes	80 (<i>n</i> = 5)	L–M
				<i>Eucalyptus campanulata</i>	S	No	0 (<i>n</i> = 12)	
				<i>Eucalyptus microcorys</i>	R	No	0 (<i>n</i> = 8)	
				<i>Eucalyptus pilularis</i>	S/R	No	0 (<i>n</i> = 34)	
				<i>Leptospermum petersonii</i>	S	Yes	3.33 (<i>n</i> = 30)	L
				<i>Leptospermum polygalifolium</i>	S/R	No	0 (<i>n</i> = 33)	
				<i>Lophostemon confertus</i>	R	No	0 (<i>n</i> = 15)	
				<i>Rhodamnia rubescens</i>	R	Yes	87.5 (<i>n</i> = 8)	L–S
	Yarrigully Nature Reserve/Transect surveys	Woodland	High–Severe	<i>Syncarpia glomulifera</i>	R	Yes	11.03 (<i>n</i> = 29)	L–M
				<i>Syzygium oleosum</i>	R	No	0 (<i>n</i> = 13)	
				<i>Uromyrtus australe</i>	R	Yes	55 (<i>n</i> = 39)	L–S
				<i>Eucalyptus pilularis</i>	S	Yes	41.92 (<i>n</i> = 198)	L–S
				<i>Melaleuca nodosa</i>	R	Yes	100 (<i>n</i> = 50)	L–S
				<i>Melaleuca quinquenervia</i>	S/R	Yes	70.27 (<i>n</i> = 333)	L–S
				<i>Angophora subvelutina</i>	S/R	Yes	Observation only	L
				<i>Austromyrtus dulcis</i>	R	Yes	68.42 (<i>n</i> = 19)	L
				<i>Corymbia intermedia</i>	R	No	0 (<i>n</i> = 27)	
				<i>Corymbia henryi</i>	R	No	Observation only	
	DoubleDuke State Forest/Transect surveys	Eucalypt woodland	High–Severe	<i>Eucalyptus amplifolia</i> subsp. <i>amplifolia</i>	S/R	Yes	66.67 (<i>n</i> = 3)	L–M
				<i>Eucalyptus baileyana</i>	R	No	Observation only	
				<i>Eucalyptus pilularis</i>	S/R	Yes	39.72 (<i>n</i> = 141)	L–S
				<i>Eucalyptus pyrocarpa</i>	S/R	Yes	26.41 (<i>n</i> = 55)	L–S
				<i>Leptospermum polygalifolium</i>	R	Yes	8.33 (<i>n</i> = 36)	L
				<i>Leptospermum trinervium</i>	R	Yes	91.67 (<i>n</i> = 120)	L–S
				<i>Melaleuca sieberi</i>	S/R	Yes	Observation only	L–M

(Continues)

TABLE 1 | (Continued)

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
	Bundjalung National Park/ Transect surveys	Coastal heath, paperbark wetland, woodland	High–Severe	<i>Acmena hemilampra</i>	R	Yes	Observation only	L
				<i>Acmena smithii</i>	R	Yes	39.29 (<i>n</i> = 28)	L
				<i>Austromyrtus dulcis</i>	R	Yes	85.11 (<i>n</i> = 47)	L–S
				<i>Baeckea frutescens</i>	R	Yes	50 (<i>n</i> = 2)	L
				<i>Calytrix tetragona</i>	R	No	Observation only	
				<i>Corymbia heNature Reserveyi</i>	S/R	Yes	Observation only	L
				<i>Corymbia intermedia</i>	R	Yes	Observation only	L
				<i>Eucalyptus pilularis</i>	S/R	Yes	35.83 (<i>n</i> = 187)	L–H
				<i>Eucalyptus planchoniana</i>	S/R	Yes	57.89 (<i>n</i> = 38)	L–H
				<i>Eucalyptus robusta</i>	R	Yes	Observation only	L
				<i>Eucalyptus tindaliae</i>	R	Yes	63.33 (<i>n</i> = 60)	L
				<i>Homoranthus virgatus</i>	S/R	Yes	18.75 (<i>n</i> = 32)	L
				<i>Leptospermum juniperinum</i>	R	No	Observation only	
				<i>Leptospermum livesiidegi</i>	S/R	Yes	83.33 (<i>n</i> = 60)	L–M
				<i>Leptospermum polygalifolium</i>	R	Yes	30 (<i>n</i> = 69)	L
				<i>Leptospermum semibaccatum</i>	R	Yes	29.03 (<i>n</i> = 31)	L
				<i>Leptospermum speciosum</i>	R	Yes	Observation only	L
				<i>Leptospermum trinervium</i>	R	Yes	80.88 (<i>n</i> = 68)	L–S
				<i>Leptospermum whitei</i>	R	Yes	17.04 (<i>n</i> = 135)	L–M
				<i>Lophostemon suaveolans</i>	S/R	Yes	Observation only	L
				<i>Melaleuca alternifolia</i>	R	Yes	100 (<i>n</i> = 1)	L
				<i>Melaleuca nodosa</i>	R	Yes	83 (<i>n</i> = 162)	L–S
				<i>Melaleuca quinquenervia</i>	S/R	Yes	70.21 (<i>n</i> = 752)	L–S
				<i>Melaleuca linearis</i>	S	Yes	Observation only	L–M
				<i>Melaleuca salignus</i>	S/R	Yes	16.67 (<i>n</i> = 60)	L–H
				<i>Melaleuca sieberi</i>	S/R	Yes	46.51 (<i>n</i> = 43)	L–M
				<i>Melaleuca squamea</i>	S/R	Yes	50 (<i>n</i> = 16)	L–M
				<i>Ochrospermum citriodorum</i>	R	No	Observation only	

(Continues)

TABLE 1 | (Continued)

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
Chatsworth Hill Nature Reserve/ Walkthrough surveys		Woodland, paperbark wetland	Moderate–Severe	<i>Aemena smithii</i>	R	Yes	25 (<i>n</i> = 4)	L
				<i>Corymbia intermedia</i>	S	No	0 (<i>n</i> = 2)	
				<i>Eucalyptus pilularis</i>	S/R	Yes	8 (<i>n</i> = 45)	L
				<i>Eucalyptus planchoniana</i>	S/R	Yes	4.65 (<i>n</i> = 43)	L-M
				<i>Leptospermum petersonii</i>	R	Yes	33.33 (<i>n</i> = 3)	L
				<i>Leptospermum polygalifolium</i>	R	No	0 (<i>n</i> = 15)	
				<i>Leptospermum trinervium</i>	S/R	Yes	31.25 (<i>n</i> = 16)	L-M
				<i>Lophostemon suaveolans</i>	S/R	No	0 (<i>n</i> = 7)	
				<i>Melaleuca alternifolia</i>	R	No	0 (<i>n</i> = 1)	
				<i>Melaleuca nodosa</i>	R	Yes	70 (<i>n</i> = 24)	L-S
				<i>Melaleuca quinquenervia</i>	S/R	Yes	82.73 (<i>n</i> = 110)	L-S
				<i>Melaleuca salignus</i>	S/R	Yes	66.67 (<i>n</i> = 15)	L-M
				<i>Melaleuca sieberi</i>	R	Yes	80 (<i>n</i> = 20)	L-S
				<i>Melaleuca styphelioides</i>	R	Yes	60 (<i>n</i> = 5)	L
Banyabba Nature Reserve/ Walkthrough surveys		Woodland	Moderate–Severe	<i>Syncarpia glomulifera</i>	S/R	No	0 (<i>n</i> = 32)	
				<i>Syzygium oleosum</i>	R	Yes	25 (<i>n</i> = 4)	L
				<i>Waterhousea floribunda</i>	R	No	0 (<i>n</i> = 1)	
				<i>Corymbia henryi</i>	S/R	No	0 (<i>n</i> = 13)	
				<i>Eucalyptus baileyana</i>	R	No	0 (<i>n</i> = 3)	
				<i>Eucalyptus glauca</i>	S/R	No	0 (<i>n</i> = 1)	
				<i>Leptospermum trinervium</i>	R	Yes	14.71 (<i>n</i> = 34)	L-S
				<i>Melaleuca nodosa</i>	R	Yes	50 (<i>n</i> = 40)	L-S

(Continues)

TABLE 1 | (Continued)

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
	Gibraltar & Washpool National Park/ Walkthrough surveys	Warm temperate rainforest, Wet sclerophyll, coachwood rainforest	Low–Severe	<i>Acmena smithii</i>	R	No	0 (<i>n</i> = 5)	L–S
				<i>Archirhodomyrtus beckleri</i>	R	No	20.9 (<i>n</i> = 67)	
				<i>Eucalyptus campanulata</i>	R	No	0 (<i>n</i> = 8)	
				<i>Eucalyptus olida</i>	R	No	0 (<i>n</i> = 5)	
				<i>Eucalyptus pilularis</i>	S/R	No	0 (<i>n</i> = 18)	
				<i>Eucalyptus tindaliae</i>	R	No	0 (<i>n</i> = 3)	
				<i>Leptospermum polygalifolium</i>	R	No	0 (<i>n</i> = 1)	
				<i>Leptospermum trinervium</i>	R	Yes	11.54 (<i>n</i> = 26)	
				<i>Rhodamnia rubescens</i>	R	No	90 (<i>n</i> = 70)	
				<i>Backhousia sciadophora</i>	R	Yes	20 (<i>n</i> = 5)	
	Burnt Down Scrub Nature Reserve/ Plot based assessments	Severe		<i>Gossia bidwillii</i>	R	Yes	100 (<i>n</i> = 1)	L
				<i>Backhousia sciadophora</i>	R	Yes	50 (<i>n</i> = 2)	M
				<i>Gossia bidwillii</i>	R	No	0 (<i>n</i> = 5)	
				<i>Lophostemon confertus</i>	R	No	0 (<i>n</i> = 1)	L
				<i>Acmena smithii</i>	R	Yes	25 (<i>n</i> = 4)	
				<i>Backhousia myrtifolia</i>	R	No	0 (<i>n</i> = 1)	
				<i>Gossia bidwillii</i>	R	No	0 (<i>n</i> = 1)	
				<i>Lophostemon confertus</i>	R	No	0 (<i>n</i> = 1)	S
				<i>Rhodamnia rubescens</i>	R	Yes	100 (<i>n</i> = 2)	
				<i>Tristaniaopsis laurina</i>	R	Yes	100 (<i>n</i> = 1)	
	New England National Park/ Plot based assessment	Severe		<i>Rhodamnia rubescens</i>	R	Yes	100 (<i>n</i> = 1)	L
				<i>Syzygium australe</i>	R	Yes	25 (<i>n</i> = 4)	L

(Continues)

TABLE 1 | (Continued)

State	Location & survey type	Vegetation type	Fire severity	Species assessed	Regeneration type	Rust infection	Percentage trees infected (Trees assessed)	Infection levels
	Nymboi-Binderay National Park/Plot based assessment		Severe	<i>Acmena smithii</i>	R	No	0 (<i>n</i> = 1)	
				<i>Rhodamnia rubescens</i>	R	Yes	100 (<i>n</i> = 4)	M
				<i>Syzygium australe</i>	R	No	0 (<i>n</i> = 1)	M
				<i>Syzygium oleosum</i>	R	No	0 (<i>n</i> = 1)	M
	Yabbra National Park/Plot based assessment		Severe	<i>Acmena ingens</i>	R	No	0 (<i>n</i> = 1)	
				<i>Backhousia myrtifolia</i>	R	No	0 (<i>n</i> = 1)	
				<i>Syzygium australe</i>	R	No	0 (<i>n</i> = 2)	
				Survey Area 4				
	Central Coast NSW	Kiwarrak State Forest/Transect surveys	Low–Moderate	<i>Melaleuca nodosa</i>	R	Yes	100 (<i>n</i> = 50)	L-H
				<i>Melaleuca nodosa</i>	R	Yes	100 (<i>n</i> = 50)	L-H
	Wallaby Point/Transect surveys	Woodland	High	<i>Melaleuca nodosa</i>	R	Yes	100 (<i>n</i> = 50)	L-H
				<i>Melaleuca salignus</i>	R	Yes	100 (<i>n</i> = 2)	M-H
	Nabiac (Fire in 2018)	Coastal heath	Low	<i>Melaleuca nodosa</i>	R	Yes	96 (<i>n</i> = 50)	L-H
				<i>Melaleuca nodosa</i>	R	Yes	100 (<i>n</i> = 50)	L-H
	Saltwater National Park/Transect & Walkthrough surveys	Coastal heath, Littoral rainforest	High	<i>Syzygium paniculatum</i>	R	No	0 (<i>n</i> = 5)	
	McClymont Creek/Transect surveys	Coastal heath	High	<i>Melaleuca nodosa</i>	R	Yes	100 (<i>n</i> = 50)	L-H
	Darawank Nature Reserve/Transect surveys	Woodland	High	<i>Melaleuca quinquenervia</i>	R	Yes	100 (<i>n</i> = 50)	L-H
				<i>Melaleuca ericifolia</i>	R	No	0 (<i>n</i> = 1)	

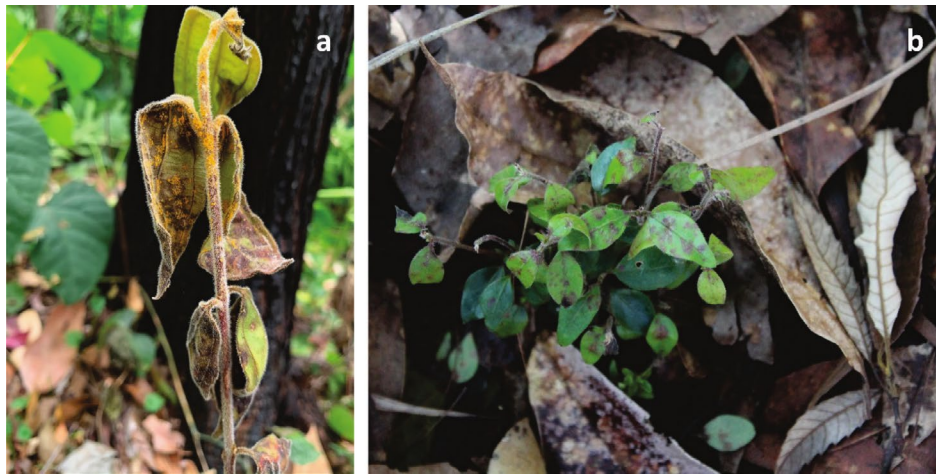


FIGURE 2 | Reshooting *Rhodamnia rubescens* (a) and *Uromyrtus australis* (b) following wildfires in Gondwana Rainforest in 2019/2020. *Austropuccinia psidii* infection on the new shoots and young foliage of reshoots causes decline and death of recovering trees.

particularly in the lower canopy, disease levels declined rapidly, with only minor disease symptoms detected after 3 months and no symptoms after 4 months.

3.2 | *Melaleuca nodosa*

3.2.1 | Yarringly Nature Reserve

Symptoms of *A. psidii* were first detected in March 2020, with 58% of reshooting fire-affected trees infected, peaking with 87.5% of trees infected in April 2020 (Figure 3). Disease levels remained high until June 2020 before declining, peaking again in September and November with 63.04% and 91.11% of assessed trees infected respectively. All 50 trees assessed had disease symptoms recorded over the course of the study.

Tree deaths associated with repeated *A. psidii* infection of reshoots were first recorded in April 2020. By the final assessment in 2022, 24 (48%) of the 50 trees had died. Twenty-one of these dead trees had disease on all new growth at least once during the assessment period. Twenty-three of the 26 trees still alive at the final assessment had *A. psidii* associated reshoot dieback. Flowering/fruitleting was assessed in August and November 2020 and again in January 2022 with two (4%), four (6%) and four (6%) trees with flowers or seed capsules, respectively. Flowering levels on these trees were rated as moderate with 26%–50% of branches assessed as having flowers or seed capsules present.

3.2.2 | Bundjalung National Park

Disease levels on *M. nodosa* peaked in May and June 2020, with the lowest levels recorded in spring and early summer (December), increasing again in late summer and autumn (March, April 2021) (Figure 3). Despite all trees having active flush in January 2021, no disease was present. In June 2021, the number of trees infected was low, but disease incidence on any new flush was high. Low levels of disease at the August (6%), December (0%) 2020 and June (14%), July (6%)

2021 assessments were primarily due to the absence of susceptible growth.

Infection resulted in repeated dieback of growing tips and complete reshoot death over time (Figure 4). Ninety-two percent of trees had some level of dieback recorded; 74% had >50% of branches with dieback at some time over the assessment period. Only four trees (8%) were found to be symptom-free throughout the assessment period. No tree deaths were recorded.

In September 2020, 62% of trees had some flowers present; 55% low abundance and 20.7% high abundance. An additional assessment in November 2020, identified 60% of trees with capsules present following flowering. Of these trees, 83% had low levels of capsule abundance and 16% with abundant levels. In January 2022, 14% of trees had capsule present, with only two trees (4%) having abundant capsules present.

Additional surveys of *M. nodosa* populations in Bundjalung National Park were conducted (September 2020) to assess the influence of *A. psidii*-related dieback on flower production (Figure 5). One hundred plants were randomly selected and assessed for branch dieback (Low = 0%–40%, Moderate = 41%–60%, High = 61%–80%, Severe = 81%–100% branches with dieback) and flowering levels (0–4 rating: 1 = 1%–25%, 2 = 26%–50%, 3 = 51%–75%, 4 = 76%–100% of branches with flowers or buds). Fifty-three percent of trees had dieback on >60% of total branches, with reduced flowering levels in comparison to trees with <40% branches affected by dieback. Flowers were absent on 5.7% of severely affected trees.

3.2.3 | Central Coast, NSW

Five sites were established in September 2020 for monthly monitoring of *A. psidii* impacts on fire-affected *M. nodosa* until February 2021, with a final assessment in May 2021 (Table 2). Disease levels were highest during warmer months of January and February 2021. In some months, the absence of susceptible new growth on trees determined disease levels rather than climatic conditions.

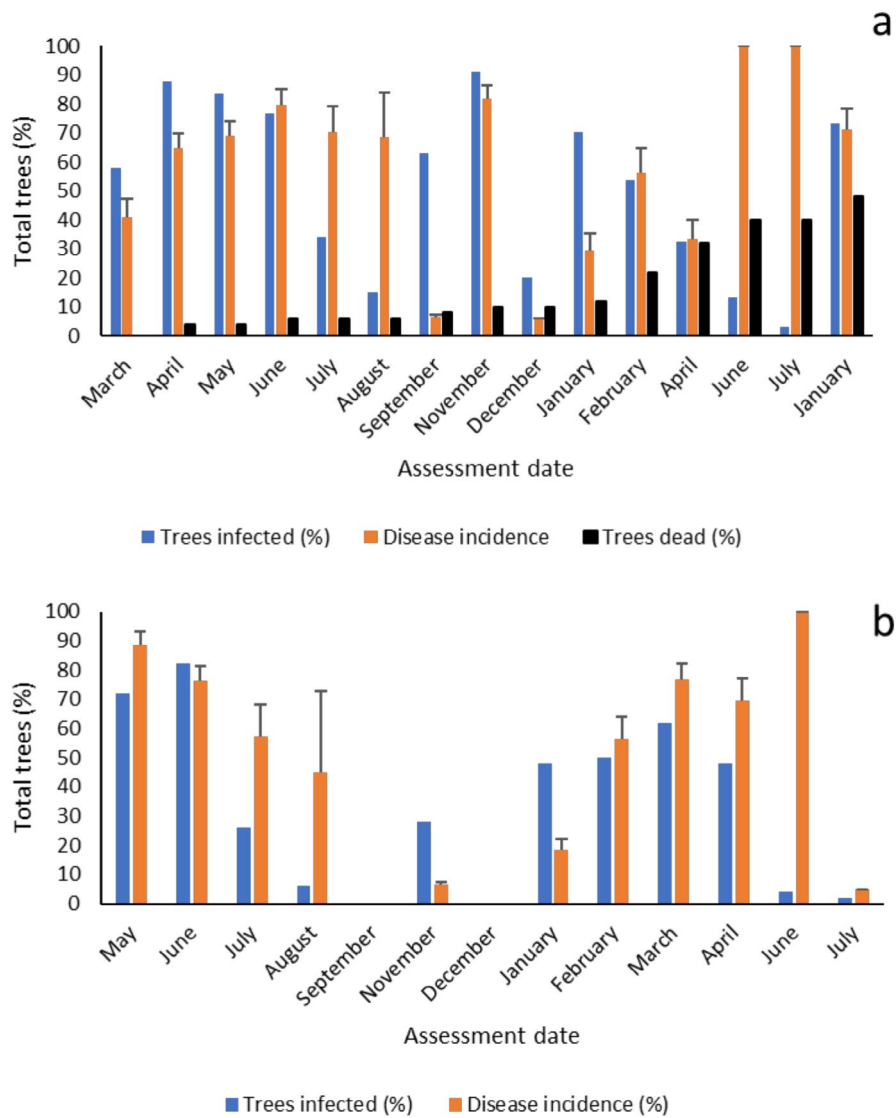


FIGURE 3 | Reshooting *Melaleuca nodosa* trees in fire-affected areas of northern New South Wales; (a) Yarrungully Nature Reserve, assessed from March 2020 to July 2021 with a follow-up assessment in January 2022 and (b) Bundjalung National Park, assessed from May 2020 to July 2021 with a follow-up assessment in January 2022 for *Austropuccinia psidii* infection symptoms with the percentage of trees affected, average incidence of disease per tree (error bars = standard error) and percentage of dead trees over time.



FIGURE 4 | Reshooting *Melaleuca nodosa* has been severely affected by *Austropuccinia psidii* (a), resulting in dieback (b) of shrubs and small trees recovering post 2019/2020 wildfires.

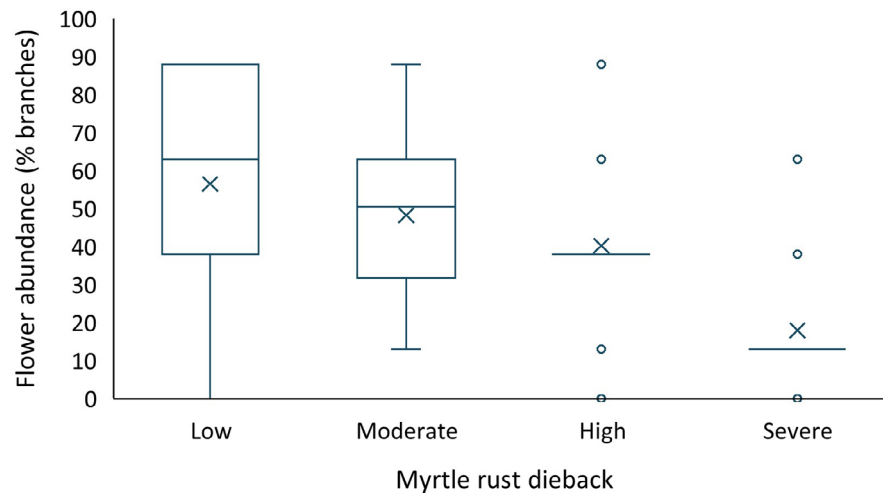


FIGURE 5 | *Melaleuca nodosa* flowering levels relating to the impact of myrtle rust (*Austropuccinia psidii*) based on levels of branch dieback observed in Bundjalung National Park, New South Wales, Survey Area 3. (Low = 0%–40%, Moderate = 41%–60%, High = 61%–80%, Severe = 81%–100% branches with dieback).

TABLE 2 | *Austropuccinia psidii* infection and disease impact levels, based on shoot dieback, on reshooting *Melaleuca nodosa* following fires in the Central Coast of New South Wales region assessed from September 2020 to May 2021.

Location	Assessment	Assessment month 2020/2021						
		Sept	Oct	Nov	Dec	Jan	Feb	May
McClymont Creek	Infected trees (%)	0	0	32	1.4	62	98	0
	Trees with shoot dieback (%)	100	0	90	90	88	98	100
	Trees with flower/fruit (%)	64	68	0	0	0	18	0
Saltwater	Infected trees (%)	0	20	72	20	96	88	4
	Trees with shoot dieback (%)	86	22	80	36	86	84	100
	Trees with flower/fruit (%)	0	38	0	0	0	0	0
Wallaby Point	Infected trees (%)	26	52	92	82	95.74	11.11	2.56
	Trees with shoot dieback (%)	88	20	92	84	97.87	97.78	100
	Trees with flower/fruit (%)	4	0	0	0	0	0	0
Knappinghat	Infected trees (%)	66	18	82	38	98	60	28.89
	Trees with shoot dieback (%)	98	6	92	88	98	100	100
	Trees with flower/fruit (%)	24	0	0	0	0	0	0
Kiwarrak	Infected trees (%)	66	18	82	38	98	60	28.89
	Trees with shoot dieback (%)	98	6	92	88	98	100	100
	Trees with flower/fruit (%)	24	0	0	0	0	0	0

All trees across sites had some level of infection and dieback. Tree deaths were greatest at the Kiwarrak site, with 56% of trees dead at the final assessment. Ten percent of trees at Knappinghat and 20% of trees at Wallabi Point were dead at the final assessment. Some level of shoot or new growth dieback was recorded on every tree at all sites during the assessments. Flowers were recorded on trees at all sites (Table 2). However, at the final assessment there was no evidence of fruit/capsule present at any of the five Central Coast sites.

3.3 | *Melaleuca quinquenervia*

3.3.1 | Yarrungully Nature Reserve

Large diameter (> 20 cm DBH) *M. quinquenervia* were affected by severe fire, with full canopy consumption. Symptoms of *A. psidii* were first detected in April 2020, with 44% of the 50 labelled trees infected (Figures 6 and 7). Disease levels, based on trees infected and average disease incidence per infected tree,

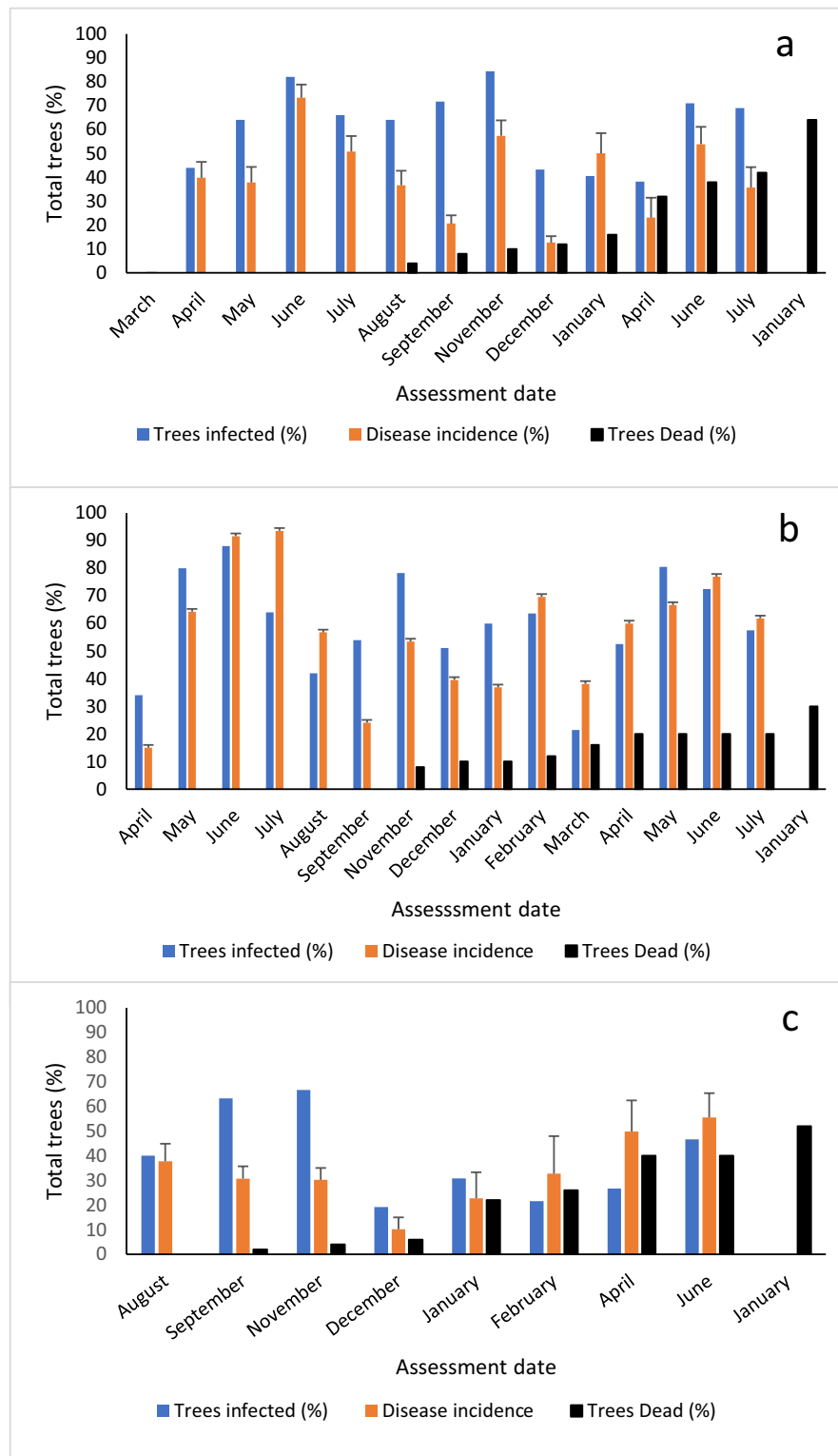


FIGURE 6 | Reshooting *Melaleuca quinquenervia* trees in fire-affected areas of New South Wales, Yarrungully Nature Reserve (a) assessed from March 2020 to July 2021 with a follow-up assessment made in January 2022, Bundjalung National Park Plot 1 (b) assessed from April 2020 to July 2021 with a follow-up assessment made in January 2022 and Plot 2 (c), assessed from August 2020 to July 2021 with a follow-up assessment made in January 2022, assessed for *Austropuccinia psidii* infection symptoms with the percentage of trees affected, average incidence of disease per tree and percentage of dead trees over time. Error bars = standard error.

peaked in June 2020 before declining and peaking again in November 2020, with 84.44% of trees infected and an average disease incidence level of 57.37% (± 6.47). Disease levels declined

again in December 2020 and January and April 2021, before another increase in the cooler months of June and July 2021 (70.97% and 68.96% of trees infected, respectively).



FIGURE 7 | Severe wildfires affected *Melaleuca quinquenervia* across a range of environments. Reshooting of trees indicated recovery, but these reshoots were impacted by *Austropuccinia psidii*, resulting in dieback and eventual tree death (a, b). *Austropuccinia psidii* repeatedly infected the new growing shoots (c, d) as trees tried to recover.

Tree deaths were first recorded in August 2020 (4%), increasing to 32% in April, 42% in July 2021 and 64% of trees were dead by the final assessment in January 2022. All dead trees had some level of *A. psidii* infection recorded during the assessment period. Six of these trees had only low disease levels recorded (< 30% disease incidence) suggesting other factors probably contributed to tree death. Insect damage was also observed on all trees, particularly during the spring months, with mirids (*Eucorcoris suspectus* (Hemiptera: Miridae)) causing damage to reshoots, often in combination with myrtle rust. All remaining living trees have had some level of infection recorded on susceptible foliage, primarily in the lower canopy reshoots.

Flowering was observed on eight of the 50 trees (16%). No trees had abundant (rating 4) flowers, but four trees had moderate levels of flowering. All eight of the flowering trees had some level of *A. psidii* infection recorded over the assessment period, two with high disease incidence levels (> 50% of susceptible foliage). Infection on these trees, however, was limited to the lower canopy with no evidence of infection or dieback in the upper canopies.

3.3.2 | Bundjalung National Park

Two monitoring plots were established to assess the impact of *A. psidii* on *M. quinquenervia* within fire-affected sites in Bundjalung National Park. Fire damage was severe, with full canopy consumption. Disease symptoms were identified in both plots. Insect damage, primarily mirid, was also evident at various times during the assessments.

3.3.2.1 | Plot 1. This site was dominated by small diameter trees (<20cm DBH) growing along the river's edge. *Austropuccinia psidii* symptoms were identified at all assessments (Figure 7). Trees infected and average disease incidence per tree increased from 34% and 15% (± 3.66) respectively in April to 88% and 91.59% (± 3.07) in June, before the number of diseased trees declined in July 2020, despite disease incidence scores remaining high during this month (93.54% (± 3.01)). Diseased trees and infection incidence declined in August 2020. Other disease peaks occurred in November 2020 and February and May 2021. Disease incidence per tree followed similar patterns but with an extended peak in June and July 2020 (Figure 6).

Tree deaths (8%) were first observed in November 2020, 7 months after symptoms were first recorded. This increased to 20% by April 2020 and 30% at the final assessment in January 2022. Flowering was observed on three trees (6%), one with moderate levels of flowering and two with low levels. While all three trees had some level of *A. psidii* infection symptoms, disease incidence levels were < 10%.

3.3.2.2 | Plot 2. This plot consisted of large diameter (>20cm DBH), overstorey trees growing as a monoculture stand on the river floodplain, inundated with water for much of the assessment period. Fire damage was severe, with full canopy consumption.

Eighty-eight percent of trees had symptoms of *A. psidii* infection at some stage during the assessment (Figure 6). Of the 26 trees that died (52% of total trees), only three lacked evidence of infection. Of the trees that remained alive, *A. psidii* symptoms were observed on all but four of the 24 trees. Approximately 45% of living

trees had moderate to severe disease incidence levels ($\geq 50\%$ foliage with symptoms) at some time over the assessment period.

Flowering was observed on six trees (12%), two with moderate to abundant flowering. Those trees that did produce flowers had either low or no evidence of *A. psidii* infection ($< 10\%$ disease incidence).

4 | Discussion

Austropuccinia psidii impacted the regeneration of Myrtaceae species in different ecosystems recovering from the 2019/20 wildfires. This included coastal heath, woodland and swamp environments, littoral and notophyll vine forests, inland paper bark swamp ecosystems, inland eucalypt woodlands, wet sclerophyll and rainforest ecosystems as far west as the Great Dividing Range. However, no evidence of *A. psidii* was identified in surveys of fire-affected areas south from Ulladulla in southern NSW. Several species in this area are known to be susceptible (Carnegie and Lidbetter 2012; Soewarto et al. 2019), including *L. trinervium*. Carnegie et al. (2016) also reported severe myrtle rust-associated dieback on *R. rubescens* in Batemans Bay. Based on recent epidemiology studies in New Zealand, climatic conditions are likely to be suitable in southern NSW for disease development, at least for the spring and summer months (Beresford et al. 2020). It is possible that our survey times did not occur during a period when myrtle rust was most active in the region, despite the conditions being considered optimum, or recovery of the pathogen population was slower than what was observed in northern NSW and South East Queensland. We recommend more surveys for myrtle rust in south-eastern NSW into eastern Victoria to determine the impact in this region.

Our surveys discovered new Australian host species, *L. speciosum*, *E. piperita*, *E. pyrocarpa* and *E. amplifolia* subsp. *amplifolia*, adding to the growing list of species in Australia to become impacted by this invasive species. Of the eucalypts surveyed, *E. pilularis* and *E. planchoniana* were the most affected by *A. psidii*, with seedling infection, dieback and deaths recorded. Disease-free seedlings were also identified, suggesting potential resistance in these two species of *Eucalyptus*. Similarly, disease-free and infected reshooting trees were observed for both *E. pilularis* and *E. planchoniana*. Interestingly, infection levels on *E. pilularis* epicormic shoots decreased with increasing height, with shoots higher in the canopy free of disease or dieback symptoms, even when shoots closer to the ground were heavily infected. This influence of canopy height on disease development has previously been reported in eucalypt plantations in Brazil (Zauza et al. 2010), with incidence and severity declining in taller trees. However, this pattern is not apparent in other species, including *M. quinquenervia* and rainforest species like *Syzygium corynanthum* (Pegg et al. 2017).

In fire-affected Gondwana Rainforests, *A. psidii* impacts were commonly identified on *R. rubescens*. While some variability in disease levels was identified, there was no evidence of resistant individuals. The variability in susceptibility does, however, warrant further investigation to inform future conservation and breeding strategies. While in this case the focus was on

fire-affected trees, *R. rubescens* was identified as being highly susceptible soon after *A. psidii* was first detected in Australia (Carnegie and Lidbetter 2012; Pegg, Giblin, et al. 2014) and studies across the host range (Carnegie et al. 2016; Fensham et al. 2021), in the absence of any specific disturbance event, confirmed the significant impact on *R. rubescens* populations. Once considered a common species, it is now listed under the Commonwealth EPBC Act 1999 as Critically Endangered because of myrtle rust (Conservation Advice *Rhodamnia Rubescens* 2020).

Other fire-affected rainforest species to be impacted were *Archirhodomyrtus beckleri*, *Backhousia sciadophora* and *Uromyrtus australis*, all known to be susceptible to infection in the absence of disturbance events (Pegg, Giblin, et al. 2014). *Uromyrtus australis* is found only in northeastern NSW on the Nightcap Range, with an estimated 800–1000 plants left that occur across 45 locations (NSW National Parks and Wildlife Service 2003). Over 50% of trees assessed were infected, with severity levels varying. Dieback occurred on $> 30\%$ of reshooting trees and symptoms were identified on fruit. Surveys in other sites, conducted under the NSW Saving Our Species Program (Kooyman 2021), assessed 14 of the 20 known genets affected by fire at Mt. Jerusalem in 2019–20. The authors reported *A. psidii* infection on 85% of plants, 33% with low levels of impact, 50% with moderate levels and 17% with high levels of impact. The study was then extended to include 40 locations within Nightcap National Park, concluding that the health and reproductive fitness of the species is in decline due to myrtle rust impacts on regenerating plants. Subsequent surveys (2020–21) found 100% of plants with myrtle rust impact, 15% with low levels, 42% moderate and 42% with high levels. A continued decline in flower and fruit production was also reported (Kooyman 2021).

In coastal heath and woodlands, *Melaleuca nodosa* was highly susceptible to myrtle rust, impacting post-fire regeneration. *Austropuccinia psidii* infection and dieback were identified in all populations assessed in northeast and Central Coast NSW, including the shrub-like form in coastal heath communities and the small-tree form in woodlands. Just under half the trees assessed in Yarrungully Nature Reserve were dead at final assessment. Tree deaths were also recorded in three of the five NSW Central Coast populations. No tree deaths were recorded in Bundjalung National Park, despite significant levels of infection and dieback. Although not dead, trees with dieback were unable to compete with more disease-tolerant Myrtaceae (*Leptospermum polygalifolium*) or non-Myrtaceae (*Acacia* spp.), becoming smothered under a thick canopy of these other species. The susceptibility of *M. nodosa* and the impact of *A. psidii* on populations recovering post-wildfire has previously been reported (Pegg et al. 2020) and, like that study, there was evidence of surviving trees at all sites. The number of these surviving trees was low, but it may indicate disease tolerance or possible resistance within populations. However, the consequence of this decline in population size, and presumably genetic diversity, is unknown. Without pre-rust population data, long-term consequences of diversity changes may be challenging to determine.

Flower and fruit development of *M. nodosa* were affected by *A. psidii* infection, with declines recorded at all sites. Hewitt et al. (2014a), studying *Melaleuca* species in 2011/12 and prior to significant impacts being recorded from myrtle rust in native

ecosystems, identified that within populations of *M. nodosa*, 68%–78% of plants flowered each year. This compares to the 6% of trees we observed at Yarrungully Nature Reserve and 14% at Bundjalung National Park. Despite flowering occurring widely at Central Coast NSW sites at initial assessments in our study, no fruits were observed in subsequent assessments. It is unknown if this relates to unsuccessful pollination or if it is entirely due to myrtle rust-induced dieback.

For *Melaleuca quinquenervia* reshoots, while some site variation was observed, dieback, reduced flowering and tree deaths due to *A. psidii* infection occurred at all sites. In some cases, tree death could be solely attributed to *A. psidii* impacts. In other cases (e.g., large diameter trees in Yarrungully and Bundjalung Plot 2) additional factors appeared to contribute. Insect attack, particularly mirid bugs, adversely affected regrowth but impact levels were not quantified in this study. Interactions between *A. psidii* and insects have been reported from Florida where *M. quinquenervia* is an invasive pest. The combined impact of *A. psidii* and insects, primarily *Oxyops vitosa*, on cut stump regrowth had an additive effect on stump and reshoot mortality (Rayamajhi et al. 2010). In our study, some trees died without any evidence of myrtle rust on reshoots, suggesting that fire damage alone could have been the primary factor in tree death.

Like *M. nodosa*, *M. quinquenervia* flowering was reduced and in many cases prevented, by repeated *A. psidii* infection. Trees in Yarrungully had the highest level of flowering, but only 16% nonetheless. Pratt et al. (2005) studying the effects of folivory on *M. quinquenervia* in Florida, USA, found that undamaged trees were 36 times more likely to reproduce than herbivore-damaged trees. They also found that a single bout of herbivory caused an 80% reduction in reproductive structures the following year. They concluded that *M. quinquenervia* partially compensates for herbivory by producing new stems and replacing foliage, but this compensation results in a substantial reduction in reproduction. Unlike repeated *A. psidii* infection, herbivory did not result in shoot or tree death.

The presence of surviving and reproducing trees at each study site may be an indicator of resistance or tolerance to *A. psidii* within the existing populations of *M. nodosa* and *M. quinquenervia*. However, given *Melaleuca* species are pollinated by a wide suite of generalist insect vectors, including native and introduced honeybees, beetles and flies (Beardsell et al. 1993), a lower density of flowering may interfere with pollination, particularly in flora-diverse sites. Conversely, if resistant plants are flowering and producing viable seedlings, it is possible that natural regeneration of species within a site could occur, consisting of disease-resistant or tolerant progeny. However, the reduced number of trees flowering and potential implications on population diversity need to be considered. Likewise, the flow-on effects of reduced flowering from a pollination process and fauna food source perspective need consideration.

A significant reduction in population size through deaths or impacts that prevent flowering, like those caused by *A. psidii*, could result in reduced genetic variation within offspring and subsequent populations, potentially increasing inbreeding. Additionally, andromonoecy, a breeding system of plant species in which both separate male and hermaphrodite flowers occur

on the same plant, has been recorded for *Melaleuca* species from Australia, including *M. nodosa* (Hewitt et al. 2014b), potentially increasing the risk of inbreeding. Inbreeding populations are at a greater risk of an accumulation of deleterious mutations that can reduce the health of individuals within a species, potentially leading to extinction. Breeding within closely related individuals within a small population could result in immediate loss of fitness in the offspring, which are potentially less able to adapt to changing environments (Charlesworth and Willis 2009; Charlesworth and Charlesworth 1999; Keller and Waller 2002). The fitness costs associated with inbreeding are due to recessive deleterious alleles that confer a disadvantage on the individual possessing them (Charlesworth and Willis 2009; Charlesworth and Charlesworth 1999).

While this study provides some insight into the impacts of *A. psidii* on post-fire recovery of individual Myrtaceae species, it does not look at the broader, long-term ecological effects or other interactions. A better understanding of the consequences of multiple disturbance factors on tree and forest health should be considered to fully understand the impacts and potential management strategies that can be implemented. Halofsky et al. (2020) highlighted interactions between fire and other disturbances, such as drought and insect outbreaks, as potential primary drivers of ecosystem change. Lombardero and Ayres (2011), studying bark beetles and fires, concluded that post-fire disease or insect spread not only depends on complex environmental factors, but also relies on the spatial patterns of host tree recovery. He et al. (2021), studying interactions between fire and sudden oak death (*Phytophthora ramorum*), state that while individual forest disturbances are well studied, interactions between multiple disturbances and changes in spatial patterns of forested landscapes are rarely quantified. While we observed insect impacts on all species assessed, we did not evaluate interactions with *A. psidii*. It must be noted that many species and ecosystems that are being impacted by myrtle rust in Australia have not been influenced by recent disturbance factors. Myrtle rust is a primary cause of disturbance (Carnegie et al. 2016; Pegg et al. 2017; Meiklejohn et al. 2022; Stevenson et al. 2023).

Longer-term studies are required, including more extensive ecological assessment, detailing changes in plant community composition and consequences of any change in species diversity. Our studies have captured the decline of species over a relatively short time. Unfortunately, our study could not provide enough evidence to link fire intensity with disease severity. Due to the extent and severity of the fires, opportunities to compare sites with different burn intensities were very limited. One thing is clear though: while forests are emerging post fire, myrtle rust impacted the recovery of many Myrtaceae.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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