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RESEARCH ARTICLE

Recruitment failure of keystone trees in *Phytophthora* infested forest

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Abstract

Invasive plant pathogens cause considerable forest loss worldwide. However, little is known about how tree populations recover post-invasion. In Western Australia, *Phytophthora cinnamomi* 'dieback' affects jarrah (*Eucalyptus marginata*), with historical records of mass deaths in this keystone tree species due to infestation, resulting in permanent loss of standing forest. Historical observations of marri (*Corymbia calophylla*), a co-dominant keystone jarrah forest tree, suggest it is resistant to *P. cinnamomi*. Impacts of *P. cinnamomi* on the population dynamics of jarrah and marri are unknown. We recorded densities and stem diameters of jarrah and marri in a peri-urban forest to examine their population demographics in >60-year-old *P. cinnamomi* infestations compared with adjacent non-infested forest. While seedling (<0.5 cm stem diameter, ~2–15 cm tall) densities were not significantly different, total tree densities were 43% (jarrah) and 48% (marri) lower for infested sites. Densities of jarrah 0.5–9 and 20–29 cm stem diameters were lower within infestations. Survival probabilities of jarrah seedlings were significantly greater in *P. cinnamomi* infestations, but those of mature jarrah were not different. While average marri stem density was 49% greater within infestations, densities of small marri (<20 cm stem diameter) were lower within infestations. Survival probabilities for marri seedlings were significantly decreased in infestations, while there was greater survival probability for mature marri within *P. cinnamomi* infestations. Our data suggest recruitment of jarrah and marri has likely reduced since *P. cinnamomi* invasion. This is the first documented impact on marri, which indicates that we have been overlooking the risk of decline due to *P. cinnamomi* for this species. We stress the need for continued management and highlight the necessity of planting seedlings ~6 months old, and assisting their survival with phosphite and fertilizers, to bolster local tree populations.

KEYWORDS
Corymbia, *Eucalyptus*, overstory foundation species, *Phytophthora* dieback, recruitment failure

INTRODUCTION

Invasive plant pathogens can kill trees, causing permanent declines to populations of dominant keystone species and the ecosystem processes that they support (Boyd et al., 2013). With a global presence in forest ecosystems due to inadvertent introduction by humans, plant pathogens have been responsible for extensive deaths of many dominant forest tree species

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in the past century (Cobb et al., 2020; Rigling & Prospero, 2018; Santini et al., 2013). Oftentimes these events have been well documented at the time of plant pathogen invasion (Dell et al., 2005; Rigling & Prospero, 2018; Tsykun et al., 2022); however, long-term monitoring of tree populations following die-off events is uncommon. Consequently, the dynamics of how tree populations recover following plant pathogen invasion are little known.

The *Phytophthora* plant pathogens are major contributors to global tree decline (Burgess et al., 2019; Hansen, 2015; Scott et al., 2013, 2019; Tsykun et al., 2022). Their microscopic nature makes them difficult to manage or to remove once established (e.g., Cahill et al., 2008; Cobb et al., 2013; Frankel, 2008; Hardy et al., 2001; Jung & Blaschke, 2004). Consequently, many *Phytophthora* species are recognized as significant plant pathogens in multiple countries, where they have devastated populations of native keystone trees (Hansen, 2015; Scott et al., 2013). Most notably, *Phytophthora cinnamomi* threatens native populations of *Quercus* spp. (oak) across the Mediterranean basin (Brasier & Scott, 1994; Camilo-Alves et al., 2013), multiple forest tree species in North America (Sena et al., 2018), and *Eucalyptus* spp. across Australia (Bose et al., 2023; Davison, 2018; Peters & Weste, 1997; Tippett et al., 1985; Weste et al., 1973). *Phytophthora ramorum* is responsible for sudden oak death across North America (Grünwald et al., 2012; Rizzo et al., 2002; Rizzo & Garbelotto, 2003). Additionally, *Phytophthora multivora* is an emerging threat to *Eucalyptus* spp. and *Agonis* spp. trees in Western Australia (Scott et al., 2009), as well as *Quercus* spp. and *Fagus* spp. (beech) trees throughout riverine parts of Europe (Mrazkova et al., 2013; Scott et al., 2009).

Phytophthora cinnamomi is described as one of the world's worst pathogens due to its wide host range in a variety of ecosystems (Burgess, White, et al., 2017; Erwin & Ribeiro, 1996; Lowe et al., 2004; Shearer et al., 2004). *Phytophthora cinnamomi* is most active during warm and wet soil conditions (Cahill et al., 2008; Shearer, 2014). During these favourable conditions, it can infect plant roots by producing large numbers of motile zoospores that swim to nearby roots, where growth throughout the root typically results in root rot (Hardham, 2005; Hardham & Blackman, 2018). The pathogen has been spread by humans to at least 11 countries, on six continents (Burgess, John, et al., 2017), and is well known for its impact on native Australian ecosystems. In Australian forest, woodland, and heath ecosystems, *P. cinnamomi* can substantially simplify the plant understory and midstory layer, and these changes can persist for decades (e.g., Shearer & Tippett, 1989; Weste, 2003; Weste et al., 2002). This is primarily due to the ability of *P. cinnamomi* to persist almost indefinitely in the roots of plants, sporulating and spreading when soils are warm and wet and receding back to roots when conditions are dry (Crone et al., 2013). Thus far, unassisted recovery of susceptible plants has not been observed in up to 30-year-old infestations, as most trees that can recolonize in dry conditions are eventually killed by *P. cinnamomi* in warm and wet conditions that invariably follow (Weste, 2003; Wilson et al., 2020). The impacts of the pathogen on overstory trees in Australia are varied, where the widespread *Eucalyptus* spp. trees have varying levels of susceptibility between species and situations (e.g., Davison, 2018; Tippett et al., 1985; Weste, 1986). There is, however, a dearth of information on the variability of susceptibility of species, and this needs considerably more attention.

In southwestern Australia's globally recognized biodiversity hotspot, *P. cinnamomi* has earned the name 'biological bulldozer' for its devastating impacts on native ecosystems and the jarrah *Eucalyptus marginata* Sm. forest in particular (WWF Australia, 2004). Jarrah forest is defined by a co-dominant tree overstory of jarrah and marri *Corymbia calophylla* (Lindl.) K.D.Hill & L.A.S.Johnson (Pryor, 1959; Koch & Samsa, 2007;

Wardell-Johnson et al., 2016), both of which can persist for over 300 years. This ecosystem has experienced a reduction of ~49% of its original 4.5 million ha coverage, with deforestation primarily through historic logging, clearing for urbanization, and mining (Wardell-Johnson et al., 2015, 2016). These practices were the main vectors of *P. cinnamomi* throughout the region, moving infested soil and road gravel across the jarrah forest from as early as 1921 (Colquhoun & Hardy, 2000; Davison et al., 2019; Dell et al., 2005; O'Gara et al., 2005). By 2019, over 1.7 million ha (38%) of the remaining forest system was estimated to be infested (Massenbauer, 2019).

Phytophthora cinnamomi was found responsible for the mortality of jarrah trees in the late 1960s (Podger, 1972), and the pathogen was considered a threat to this economically important timber tree. Jarrah is more susceptible to infection when waterlogged than not waterlogged, and most jarrah deaths between 1940 and 1960 were observed within 3 years of extremely high rainfall (Davison, 2015, 2018). Large-scale jarrah deaths tend to occur on shallow soils over a perched water table where water pools around roots, lignotubers, and stem collars for long periods (Davison & Tay, 1987; Hardy et al., 1996; Podger et al., 1965; Shearer & Tippett, 1989; Waring, 1950). Forestry logging practice may have exacerbated jarrah tree decline from *P. cinnamomi*, where waterlogged soils become more likely with the removal of most large trees resulting in less drawdown of soil water. Most of the jarrah forest ecosystem has been logged at least once between 1833 and 2004, and almost all old-growth (i.e., >100 years) trees have been removed (Calver & Wardell-Johnston, 2004; Wardell-Johnson et al., 2015).

Marri trees are considered field resistant to *P. cinnamomi* infection, although roots can have low levels of colonization (Cahill et al., 1992; Tippett et al., 1985), and in pot trials, seedlings can experience considerable, but often non-lethal reductions to root mass (Croeser, 2021). Marri saplings (up to 7 years of age) can be killed by *P. cinnamomi* when water ponds around the lignotuber. Ponding likely allows the pathogen to sporulate and reach high zoospore densities and transports zoospores to the lignotuber. This results in heavy lesioning from the pathogen (often collaring) on the lignotuber, but not the roots or stem, and stops water transport through the tree leading to death of the tree (Hardy et al., 1996). While marri has not been targeted for intensive logging, the species has been affected by the logging of neighbouring jarrah trees and subsequent effects on hydrology. Despite their co-occurrence with jarrah, there are no records of mass marri deaths alongside jarrah, and many marri typically continued to survive where mass jarrah deaths occurred, with few deaths observed along infestation fronts (Davison, 2015, 2018; Shearer & Tippett, 1989).

Both the logging history and invasion of *P. cinnamomi* in the jarrah forest have likely impacted forest dynamics, in particular, tree recruitment and growth opportunities. McDougall et al. (2002) measured jarrah and marri stand densities in 20- and 50-year-old infestations and found considerably lower densities of jarrah but not marri in infestations compared to non-infested stands. Although jarrah population trends in infested stands indicated continuous recruitment, fewer small jarrah trees were observed than in non-infested forest, suggesting reduced recruitment (McDougall et al., 2002). There is evidence that marri can exhibit low levels of recolonization of infested areas (Dell & Malajczuk, 1989), suggesting a level of seedling resistance to the pathogen. Shearer et al. (2009) also found a lower basal area of jarrah forest and *Banksia* woodland trees inside infested areas, leading to lower canopy cover, but did not record sizes or presence of young trees. These few studies suggest an impact of *P. cinnamomi* on forest dynamics, but confirmation is needed. There is a need to understand the details particularly given significant climate change and forest practices in the region.

Rainfall in southwestern Australia has been steadily declining since the 1970s (Timbal et al., 2006), leading to soil conditions that are possibly less conducive to *P. cinnamomi* activity (Serrano et al., 2024; Shearer, 2014). While forestry activity has very recently ceased (2024), strict forest quarantine measures over previous decades have slowed the pathogen's spread (Dell et al., 2005). Consequently, tree populations may have begun to recover in old *P. cinnamomi* infestations. This study thus investigated (1) tree density and canopy cover, (2) successful recruitment, and (3) seedling density of jarrah and marri, comparing *P. cinnamomi*-infested and adjacent non-infested forest.

METHODS

Study area forestry and *P. cinnamomi* history

Our study sites included five peri-urban reserves within the Shire of Mundaring, Western Australia (31°54′8.37″ S 116°9′49.70″ E, 289 m altitude), which lies at the northern edge of the jarrah forest bioregion (Figure 1). This bioregion has long been home to the Whadjuk Noongar and more recently has been a critical water catchment and recreational area for people living in the city of Perth. Many jarrah forest plant species, including jarrah (djarraly in Noongar language), are endemic to the region and therefore significant for sense of place. Mundaring was first explored by European settlers in 1829, and harvest of native old-growth jarrah began as early as the 1860s (Menck, 2013; Figure 2a). It was likely that *P. cinnamomi* was introduced with the establishment of the first orchards and vineyards in

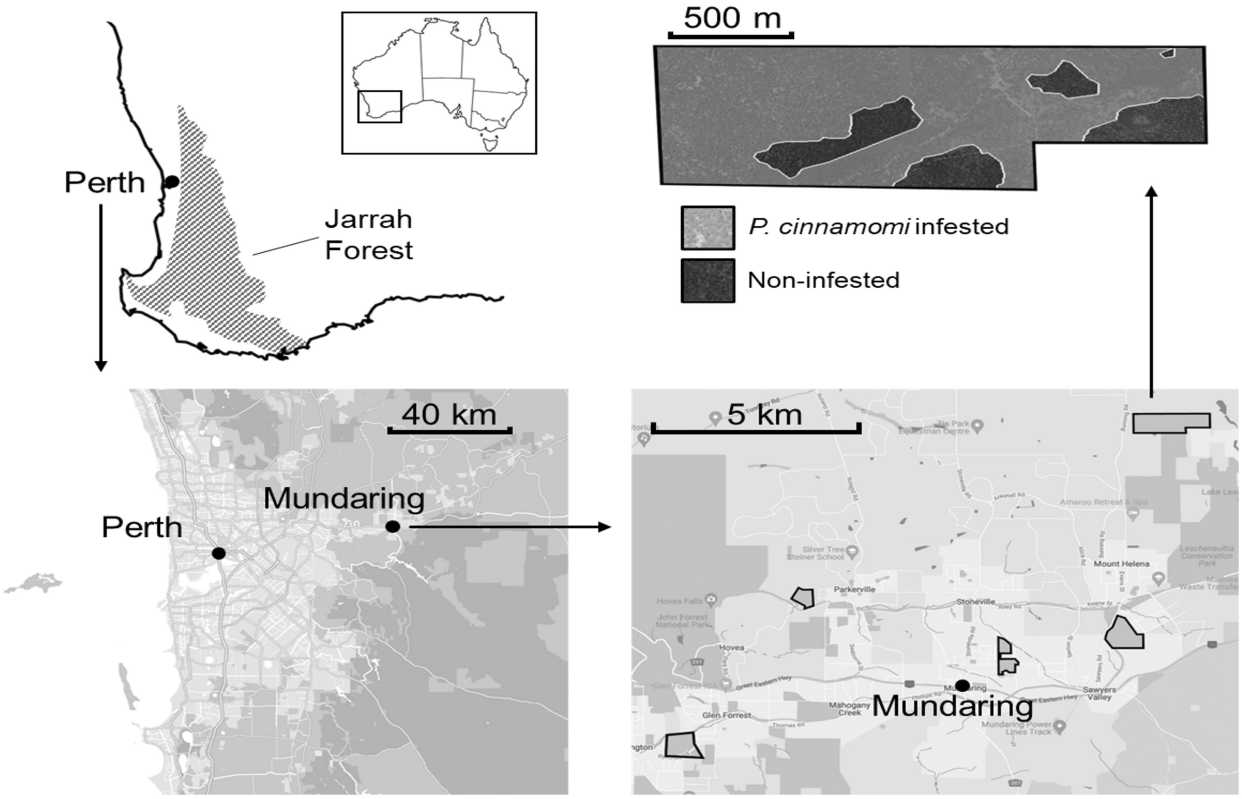


FIGURE 1 Location of the Shire of Mundaring, Western Australia, and the five peri-urban reserve study sites outlined in black. The extent of the jarrah forest bioregion is depicted top left in hatched lines. The largest infestation at Quail Street Reserve is depicted top right, showing the *Phytophthora cinnamomi* infestations.

the area in the 1880s (Menck, 2013; Newhook & Podger, 1972). Jarrah harvesting, along with gravel extraction and road laying, spread *P. cinnamomi* through the shire (Figure 2b). The town of Mundaring was settled when the Mundaring Weir construction began in the 1890s. Mundaring received exceptionally high rainfall between the 1920s and 1970s (Bureau of Meteorology, 2023; Figure 3), and Mundaring likely experienced large-scale jarrah deaths from *P. cinnamomi* during this period along with many areas of the northern jarrah forest region (Davison, 2018). Like the rest of southwestern Australia, Mundaring's total annual rainfall has decreased since the mid-1970s (Timbal et al., 2006; Mundaring Weir weather station; Bureau of Meteorology, 2023; Figure 3), with an 11% reduction in total annual rainfall over the last 50 years (1920–1970: 1124 ± 220 mm compared with 1971–2021: 1001 ± 176 mm; two-sample *t*-test $t_{97} = 3.05$, $p = 0.003$).

Our data was collected in five peri-urban reserves representative of the jarrah forest complexes Dwellingup and Yarragil; both vegetation complexes feature open forest of mixed jarrah and marri keystone tree overstory and mostly differ in their dominant understory species (Mattiske & Havel, 1998). Reserves had Dwellingup 2 phase and Murray 2 phase soils (phase and number refer to the lowest hierarchy of soil mapping according to Schoknecht et al., 2004). Vegetation complexes and soil types were not linked, with all combinations occurring between the five study reserves. All reserves featured large (>5 ha) *P. cinnamomi* infestations with equal or larger adjacent non-infested forest (Figure 1). The pathogen impact in these reserves was intermediate to high according to Shearer and Tippett (1989), where low impact describes localized death of susceptible understory shrubs, intermediate impact describes most of the susceptible understory as dead, but little to no impact to jarrah, and high impact describes most susceptible overstory and understory dead. Understory plant cover was greatly reduced in most reserve infestations, occasionally resulting in areas of open ground. Mapping based on land-use history and aerial imagery (1965–2022) shows that the *P. cinnamomi* infestations at the study sites were likely older than 60 years. In each reserve, the pathogen has killed susceptible plants (Figure 1; Grehan, 2020) and likely persists in the roots of asymptomatic plants (such as mature marri and native perennials; Crone et al., 2013; Jung et al., 2013).



FIGURE 2 Potential sources of *Phytophthora cinnamomi* introduction into urban reserves in the Shire of Mundaring, Western Australia. Photographed are examples in the Shire of Mundaring of (a) logging using saw-cut methods at Falls Road Reserve (non-infested forest) and (b) filled gravel extraction pit at Nan MacMillan reserve (*P. cinnamomi*-infested, partially restored with eastern-Australian species). Photographs: Tom Mansfield.

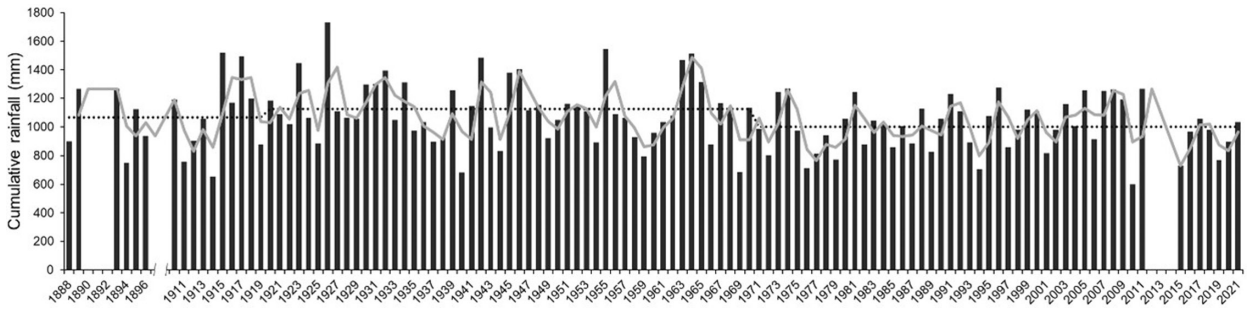


FIGURE 3 Total (cumulative) annual rainfall for the study region from 1888 to 2021 with 2 year moving average line. Gaps in columns are years where data was not collected, no data was collected between 1896 and 1910. Average total rainfall from three periods presented (dotted line); 1888–1919, 1920–1970 high rainfall period, and 1971–2021 low rainfall period. Observations were taken from the Mundaring weather station (Station 9030; Bureau of Meteorology, 2023).

Survey design

Sampling occurred along 40 strip transects that crossed *P. cinnamomi* infestation fronts, and 36 quadrats over the transects (four quadrats were excluded due to overlapping; Figure 4). Transects were 90 m long with the midline around the *P. cinnamomi* infestation active front; the central 30 m buffer around the infestation was avoided, resulting in a 30 m transect in *P. cinnamomi*-infested and a 30 m transect in adjacent non-infested forest. Stand densities of jarrah and marri were measured for 10 m on either side of the 30 m transect sections (20 × 30 m, total 600 m^2 area surveyed for each quadrat, $n = 36$; Figure 4). For each tree within these quadrats, we recorded diameter at breast height over bark (DBHOB; hereafter referred to as stem diameter) at 1.3 m high on the stem. Trees with multiple main trunks had all trunks recorded and averaged (Table S1). Any tree below 2 m tall had its stem diameter recorded in the middle of the trunk, below any forking branches. Young trees with a stem diameter <0.5 cm, ~2–15 cm tall ('seedlings') were not counted among these individuals, but instead were counted within a smaller area of 2 × 30 m strip running along the transect ($n = 40$; Figure 4).

We recorded canopy cover using a spherical crown densiometer measured at six points along the transect, beginning at 20 m from the infestation active front and repeated every 5 m thereafter; densiometer recordings were averaged for each transect ($n = 40$; Figure 4). Densiometer recordings taken beneath dense *Banksia sessilis* (Knight) A.R.Mast & K.R.Thiele thickets were excluded as *B. sessilis* is a mid-story plant.

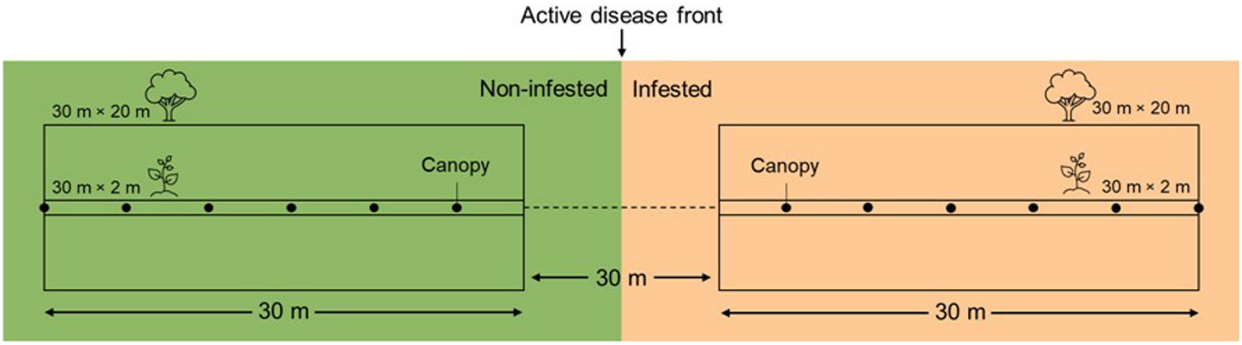


FIGURE 4 Survey design representing paired quadrats straddling *Phytophthora cinnamomi* active disease fronts; *P. cinnamomi* non-infested left (green), and *P. cinnamomi*-infested right (orange). Central dotted line represents 30 m non-studied buffer. Large rectangles represent 30 × 20 m quadrats used to count jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) stem densities of trees ≥2 cm stem circumference. Long, skinny rectangles represent 2 × 30 m strip quadrats used to count densities of jarrah and marri seedlings: plants with stem diameter <0.5 cm, ~2–15 cm tall. Black dots represent six canopy cover measurements.

Data analysis

Jarrah and marri tree densities, and overall canopy cover

To test for the impact of *P. cinnamomi* infestation on tree densities, tree stem size, seedling densities (jarrah and marri as dependent variables in separate analyses), and canopy coverage (each measure as a dependent variable in separate analyses), we fitted linear mixed effect models using the 'lme4' (ver 1.1-31 Bates et al., 2014) and 'lmerTest' (ver 3.1-3 Kuznetsova et al., 2015) packages in R (R Core Team, 2018) with *P. cinnamomi* infestation ('zone'), vegetation complex (Dwellingup and Yarragil; Mattiske & Havel, 1998), and soil type (Dwellingup 2 phase and Murray 2 phase; Schoknecht et al., 2004) included as fixed factors. Models included random factors of transect nested within reserve. We undertook model selection based on Aikaike's Information Criteria (AIC), selecting the lowest AIC, and keeping zone as a constant fixed effect (Burnham & Anderson, 2004). Selected models were assessed for conformity with assumptions of zero-centred residuals and homoscedasticity (Zuur et al., 2009) using qqplots in the 'DHARMa' R package (ver 0.4.6 Hartig & Hartig, 2017). Where assumptions were not met, outliers were identified where they were 1.5 times the interquartile range, and removed if they resulted in violated assumptions. We present marginal *r*-squared (MR^2) values to explain the influence of fixed factors on variance, and conditional *r*-squared (CR^2) to show the cumulative influence of fixed and random factors.

Recruitment and survival analysis

To quantify recruitment, for each tree within quadrats. Jarrah and marri stem diameter data were separately pooled into 10 cm diameter size classes to investigate the impacts of *P. cinnamomi* on different aged trees (Whitford, 2002). We also included seedling densities multiplied tenfold to represent seedling densities/600 m^2. To determine if jarrah and marri recruitment profiles differed between *P. cinnamomi* infestations and adjacent non-infested forest, we calculated Chi-squared goodness of fit (Plackett, 1983) in Microsoft Excel for each species (jarrah and marri separately). Observed values were tree densities (count data) within each size class for *P. cinnamomi* and non-infested forest zones, and expected values were calculated from the overall proportion of each size class. Only one size class and *P. cinnamomi* zone combination had <5 sample size and therefore our data met the assumptions of this test. For visualization and to improve comparison between other studies, recruitment profiles and tree densities are presented in hectares.

To estimate the survivability of trees following recruitment within *P. cinnamomi* and adjacent non-infested areas, we used the "survival" package (ver 3.2-7 Therneau & Lumley, 2015) to plot Kaplan Meier curves for jarrah and marri, using stem diameter as a measure of tree age. We present analyses both with and without seedling counts. Kaplan Meier curves with seedling counts represent the survival of seedlings, and those without seedlings represent the survival of trees. We also present hazard ratio (HR [95% CI]) values, which represent the proportion impact of the *P. cinnamomi* zone treatment to tree survival compared to the non-infested zone treatment, with a higher number than one signifying an increasing 'hazard' chance – in this case tree survival represented by tree occurrence – and a lower number than one the opposite (Abd ElHafeez et al., 2021). The traditional test to compare hazard ratios, the log-rank test (Ananthakrishnan et al., 2021), was used for survival analysis of jarrah seedlings, jarrah trees, and marri trees. However, survival curves of marri seedlings crossed,

making log-rank test inappropriate (Dormuth et al., 2022). We therefore employed a two-stage procedure to compare hazard rates of marri seedlings between *P. cinnamomi* infestation zones using the "TSHRC" package (ver 0.1-6 Qiu & Sheng, 2008). Because of this, we could not report a hazard ratio value for marri seedlings.

RESULTS

Jarrah and marri tree densities, and overall canopy cover

Jarrah tree densities were 43% lower in *P. cinnamomi* infested (167–833 jarrah trees/ha) compared to adjacent non-infested forest (100–1483 jarrah trees/ha; $F_{1,18}=8.81$, $p=0.008$, $MR^2=0.19$, $CR^2=0.26$; Table 1). However, average jarrah stem diameters (i.e., tree sizes) were not significantly different between *P. cinnamomi* (0.6–109 cm jarrah stem diameters) and adjacent non-infested forest (0.6–107 cm jarrah stem diameters; $F_{1,18}=0.28$, $p=0.603$, $MR^2=0.01$, $CR^2=0.17$; Table 1). Total marri tree densities were 48% lower in infested forest (17–1033 marri trees/ha) than in non-infested forest (17–2017 marri trees/ha; $F_{1,18}=5.19$, $p=0.035$, $MR^2=0.08$, $CR^2=0.46$) and showed high variance among reserves (Table 1). Average marri stem diameters (i.e., tree sizes) were 49% larger in infested forest (0.6–82 cm marri stem diameters) than non-infested forest (0.6–63 cm marri stem diameters; $F_{1,33}=6.90$, $p=0.013$, $MR^2=0.17$, $CR^2=0.17$; Table 1). Canopy cover for both species was 9% lower in *P. cinnamomi* infestations ($F_{1,20}=7.41$, $p=0.013$, $MR^2=0.09$, $CR^2=0.55$; Table 1) but showed high variance among transects (nested in reserve) and reserves (Table 1).

Jarrah and marri seedling densities were not significantly different between *P. cinnamomi* infested forest and non-infested forest (jarrah: $F_{1,40}=3.31$, $p=0.077$, $MR^2=0.00$, $CR^2=0.00$; marri: $F_{1,20}=1.42$, $p=0.247$, $MR^2=0.02$, $CR^2=0.38$; Table 1). Jarrah seedling densities were not different between soil types ($F_{1,40}=3.66$, $p=0.063$, $MR^2=0.15$, $CR^2=0.15$), and soil type was not selected within the optimal model for marri seedling densities. Vegetation was not selected within the optimal models for seedling densities of both species.

TABLE 1 Overstory keystone tree variables across five jarrah forest study reserves, showing a test of prediction that tree densities, tree stem diameters, and canopy cover differed between *Phytophthora cinnamomi*-infested and non-infested forests.

Overstory tree variable	Estimates (mean ± 95% CI)		df	*F*	*p*-value	MR^2	CR^2
	Non-infested	Infested					
Jarrah trees/ha	617 [467–750]	350 [217–483]	1, 18	8.81	**0.008**	0.19	0.26
Jarrah stem diameter	19 [16–21]	20 [17–22]	1, 18	0.28	0.603	0.01	0.17
Jarrah seedlings/ha	833 [500–1167]	500 [167–833]	1, 40	3.31	0.077	0.00	0.00
Marri trees/ha	450 [200–700]	233 [0–483]	1, 18	5.19	**0.035**	0.08	0.46
Marri tree stem diameter	14 [12–17]	20 [17–22]	1, 33	6.90	**0.013**	0.18	0.18
Marri seedlings/ha	1000 [500–1500]	667 [167–1167]	1, 20	1.42	0.247	0.02	0.38
Canopy cover %	73 [67–79]	66 [30–72]	1, 20	7.41	**0.013**	0.09	0.55

Note: Data are means and results are model estimates for linear mixed effect models that included sampling transect, nested within reserve as a random factor. We present estimates of tree densities here scaled to 1 ha from 600 m^2 study plots, and seedling densities scaled to 1 ha from 60 m^2 study plots. Stem diameters are cm. Three outliers were removed from 'marri tree stem diameter' recordings due to being 1.5 times the interquartile range. Statistically significant ($p<0.05$) differences between infested and non-infested data are represented in bold.

Recruitment and survival analysis

Patterns of recruitment differed significantly between *P. cinnamomi* zones for both jarrah ($\chi^2_{7,2699} = 739.02$, $p < 0.0001$) and marri ($\chi^2_{5,2836} = 562.17$, $p < 0.0001$). There were significantly fewer small jarrah (0.5–9 cm and 20–29 cm size classes) and similarly fewer young marri trees (seedlings < 0.5 cm and trees 0.5–19 cm) within infestations. In contrast, there were greater densities of marri trees >30 cm stem diameter within *P. cinnamomi* infestations (Figure 5).

Survival curve profiles between *P. cinnamomi* zones were different for tree species and the inclusion or exclusion of seedlings (Figure 6). Survival analysis showed greater survival probabilities of jarrah seedlings recruited within *P. cinnamomi* infested forest than those recruited within non-infested forest (HR = 0.89 [0.85–0.93], $p = 0.004$; Figure 6a), with survival probabilities equalized for trees over ~25 cm stem diameter. Excluding seedlings (<0.5 cm stem diameter), survival of jarrah trees was more similar between *P. cinnamomi* zones (HR = 0.87 [0.79–0.95], $p = 0.084$; Figure 6b). Mature marri showed generally greater survival within *P. cinnamomi* infestations compared with jarrah. Marri seedlings recruited within *P. cinnamomi* infested forest had decreased survival probabilities when less than ~10 cm stem diameter, but greater survival when over ~20 cm stem diameter (two-step HR comparison: $p = 0.011$; Figure 6c). Excluding seedlings, survival of marri trees was 33% greater within *P. cinnamomi* infested forest from ~15 cm stem diameter onwards (HR = 0.67, 95% CI: 0.58–0.75, $p < 0.001$; Figure 6d).

DISCUSSION

Jarrah (–43%) and marri (–48%) densities as well as canopy cover (–9%) were all significantly lower within *P. cinnamomi* infestations across five peri-urban jarrah forest sites, which can be mostly attributed to fewer young trees. However, our findings also paradoxically suggest that survival probabilities of mature trees in *P. cinnamomi* infestations were equal to (jarrah) or higher than (marri) adjacent non-infested forest, likely because of competitive release in the more sparsely vegetated infested forest. Indeed, larger marri trees were more common within infestations, evidenced by average marri stem diameters being 49% larger. Nonetheless, low overall tree densities and unsuccessful recruitment of young trees within *P. cinnamomi*-infested forest suggest that local populations may decline further without recruitment.

Recruitment failure of jarrah and marri to mature stands

Low densities of jarrah trees were expected within *P. cinnamomi* infestations due to historic mass deaths likely having a legacy effect on current populations (Calver & Wardell-Johnston, 2004; McDougall et al., 2002; Wardell-Johnson et al., 2015). However, it was mostly young trees <30 cm stem diameter underlying density differences between infested and non-infested forest, suggesting that the impact of *P. cinnamomi* is recent, that is, impacting smaller trees. *Phytophthora cinnamomi* can directly kill jarrah seedlings (Crombie et al., 1987), and reduced canopy cover within infestations may indicate reduced seed fall and seedling establishment (Cargill et al., 2019; White-Toney, 2020). Together, this may have resulted in lower densities of young jarrah trees as less seedlings became established and were recruited into mature tree populations. This finding differs from that

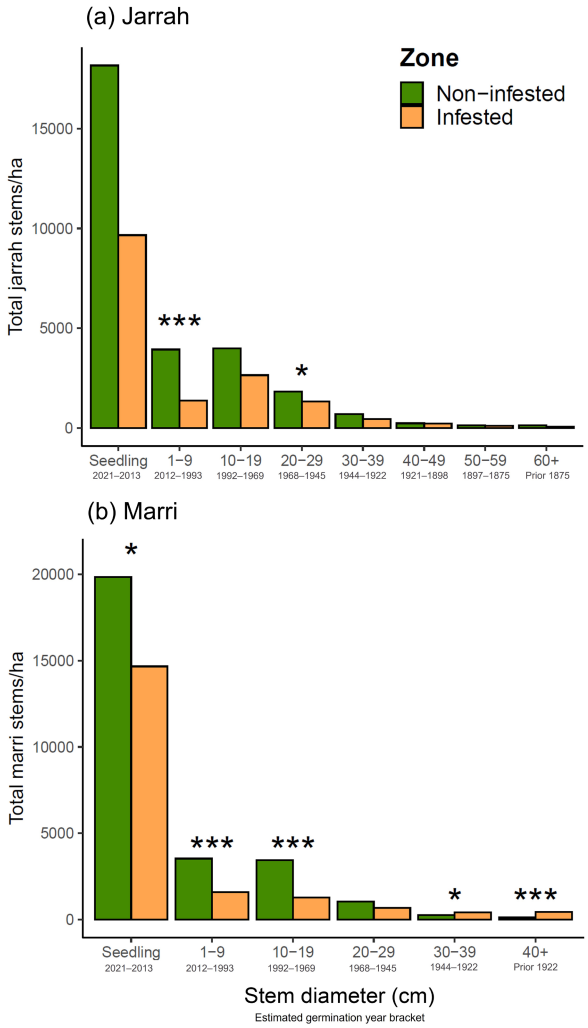


FIGURE 5 Pooled tree and seedling densities/ha of (a) jarrah (*Eucalyptus marginata*) and (b) marri (*Corymbia calophylla*), between non-infested (green) and *Phytophthora cinnamomi*-infested (orange) plots ($n = 36$). Stem diameters pooled into 10 cm diameter classes. Error bars represent 95% confidence intervals. Asterisks represent significant (*$p < 0.05$, ***$p < 0.001$) differences from Chi-square goodness of fit tests between infested and non-infested data. Seedling densities (recorded in 60 m^2 plots) were multiplied tenfold to represent tree densities (recorded in 600 m^2 plots) prior to analysis.

of McDougall et al. (2002), who suggested jarrah tree populations were recovering within infestations in another section of the jarrah forest (Myara forest block, Western Australia, approximately 70 km south of Mundaring). It is possible that jarrah recruitment failure has become more pronounced in the 20 years since observations by McDougall et al. (2002) and repeat monitoring of tree plots within Myara forest block would provide valuable insights that would complement findings of the present study.

Previous studies of jarrah forest elsewhere report no impact of *P. cinnamomi* on marri tree densities, even where there is high mortality of jarrah trees (e.g., McDougall et al., 2002; Shearer & Tippett, 1989). Additionally, marri can sometimes colonize infestations where jarrah is largely absent (Dell & Malajczuk, 1989). However, *P. cinnamomi* impacted the densities of young marri and jarrah in our study. Our observation of decreased marri tree densities within infestations and significant recruitment failure for marri (as evidenced by lack of marri trees <20 cm stem diameter) was therefore unexpected. This finding brings into question the supposed resistance of marri to *P. cinnamomi* under non-waterlogged conditions (Cahill et al., 1992;

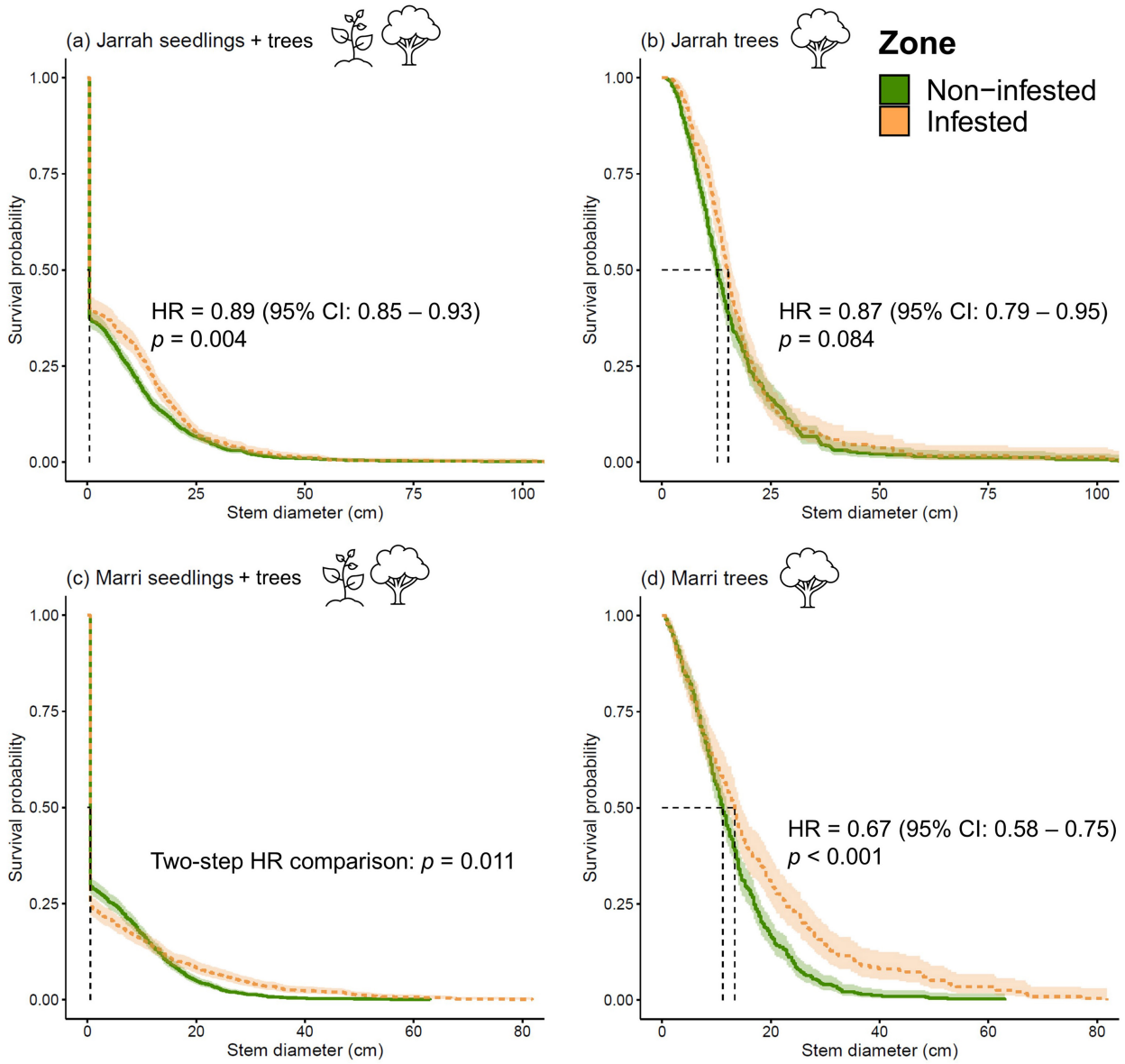


FIGURE 6 Kaplan–Meier curves of jarrah (*Eucalyptus marginata*) survival probability based on tree abundances and stem diameters (a) including seedlings and (b) only of recruited trees, and marri (*Corymbia calophylla*) survival probabilities (c) including seedlings and (d) only of recruited trees, comparing non-infested (green, solid curve) and *Phytophthora cinnamomi*-infested (orange, dotted curve) forest zones. Shaded error bars represent 95% confidence intervals. Black dotted line represents median survival. Hazard ratio (HR) represents the magnitude of the zone treatments, with a lower number signifying an increasing chance of different survivability between zones. Two-step HR comparison was used for marri seedlings (c) because of crossing survival curves.

Croeser, 2021; Tippett et al., 1985). Whether the pathogen was directly responsible for marri declines in this study or if harsh environmental conditions within *P. cinnamomi* infestations were a stronger influence is an open question worthy of future research. A combination of the two stressors is a likely scenario, as fine roots of marri can be heavily reduced by *P. cinnamomi* under temporarily waterlogged conditions (Croeser, 2021), which when followed by hot and dry summer conditions could lead to death of seedlings.

Seedling survival

Seedling densities of both jarrah and marri were unchanged within *P. cinnamomi* infestations, and jarrah seedlings in the infested forest had higher

survival potentials than those in non-infested forest. These results seem to contradict our findings of recruitment failure; however, the recorded seedlings may have been cohorts that survived the impact of *P. cinnamomi* due to conditions being unfavourable for pathogen spread and activity at that time (Crone et al., 2013). Reductions in *P. cinnamomi* activity may have allowed seedlings to avoid root loss (e.g., Crombie et al., 1987) and may also decrease the potential for emergent seedlings to encounter 'damping-off' scenarios, which is the loss of underground biomass of emerging seedlings often due to soil pathogens such as *P. cinnamomi*. It is also possible that trees within *P. cinnamomi* infestations produce more *P. cinnamomi*-resistant seedlings, as seen in *Quercus ilex* L. (holm oak) forests (Vivas et al., 2021). There is some evidence of this for jarrah (Bose et al., 2023; Stukely & Crane, 1994) but none for marri. This study was a snapshot in time and may not be representative of historic conditions that may have prevented recruitment. For example, high rainfall years (i.e., 2005–2009; Figure 3) may have contributed to waterlogged soils with increased *P. cinnamomi* activity. The pathogen can reduce root biomass of both jarrah and marri seedlings in waterlogged conditions (Croeser, 2021; Hardy et al., 1996), which could have led to many seedlings dying and thereby reducing recruitment of mature trees.

Additionally, extreme heatwave and drought events in the jarrah forest (Matusick et al., 2013, 2018) may have been more severe for seedlings within infestations where canopy cover is generally lower, and soils may be more parched in summer (Shearer et al., 2009). Taken together, while seedlings can germinate successfully within infestations, sporadic events may prevent them from consistently recruiting to adult tree populations. It is important to recognize that our 'survival' analysis was representative of tree and seedling population structure at the time of the survey, rather than quantifying actual seedling and tree survival over time. Longitudinal studies of tree recruitment or restoration within *P. cinnamomi* infestations and the influence of climatic events would be required to unravel the break-point between germination and recruitment success.

Competitive release improves mature tree survival

Older, mature marri trees >30 cm stem diameter were considerably more abundant within infestations and had higher survival than those in non-infested forest. Competitive release may have enabled marri to grow old more successfully, as there would be less competition for root space and soil resources with considerably fewer overstory trees and midstory *Banksia grandis* Willd. and *Persoonia elliptica* R.Br., which are highly susceptible to *P. cinnamomi* (Shearer et al., 2004). Additionally, jarrah tree survival and average stem diameters did not differ significantly but were marginally higher within *P. cinnamomi*-infested compared to non-infested forest. This suggests that jarrah may also experience competitive release within infestations but less so than marri. Competitive release for mature trees may be linked to declines in mean annual rainfall since the 1970s (Timbal et al., 2006) and the coincidence of sub-optimal conditions for *P. cinnamomi* to infect mature jarrah trees.

Forest recruitment failure may lead to generational declines

Our study shows that jarrah and marri recruitment failure may occur within *P. cinnamomi* infestations with lower densities of young trees compared to non-infested forest. There is evidence that jarrah are not recruiting

successfully with fewer jarrah trees of <9 cm than those 9–19 cm stem diameter, and marri are stagnating at low densities compared to adjacent non-infested areas. This forecasts potential time-delayed declines to future generations of jarrah and marri inside of these *P. cinnamomi* infestations, as fewer young trees will be available to replace older trees, and local populations may continue to decline with each generation. These patterns are representative of the long-term demographic decline termed 'extinction debt' common to long-lived and slow seeding species such as *Eucalyptus* spp. (Fowler et al., 2023; Tilman et al., 1994). Hence, jarrah and marri may be experiencing extinction debt within the studied *P. cinnamomi* reserves, and the long generation time of these trees makes this more likely (Kuussaari et al., 2009). Conditions for jarrah forest trees are becoming increasingly threatening due to climate change, resulting in canopy collapse in some areas (Matusick et al., 2013; Steel et al., 2019). This may have future implications for already reduced tree numbers in *P. cinnamomi* infestations, which could result in accelerated declines in tree populations and subsequent ecosystem functions. We emphasize the importance of repeatedly surveying tree and seedling densities across years to monitor actual recruitment to *P. cinnamomi* infested forests, to assess how tree populations are impacted by *P. cinnamomi*.

Ecosystem changes following *P. cinnamomi* infestation

Jarrah and marri provide a plethora of ecosystem services, which are likely occurring at a reduced rate under their decline in *P. cinnamomi* infestations. Both trees form mycorrhizal associations and are the primary ectomycorrhizal hosts in mixed jarrah forest systems where they are dominant trees (Brundrett & Abbott, 1991). It could be expected that with less available hosts in *P. cinnamomi* infestations that the abundance of ectomycorrhizal fungi communities may also be fewer. Additionally, canopy gaps from tree decline can result in root gaps, which may reduce local levels of ectomycorrhizal colonization as seen in *Eucalyptus gomphocephala* DC. (tuart) forests (Ishaq et al., 2013), which run along the southwestern Australia coastline parallel to the jarrah forest. Current literature suggests that ectomycorrhizal fungi abundance and diversity declines within *P. cinnamomi* infestations (e.g., Anderson et al., 2010; Corcobado et al., 2014); however, these studies are scarce. Ectomycorrhizal fungi often associate with germinants (Kariman et al., 2012) and provide important nutrient-for-carbon exchanges with jarrah and marri. Hence, if ectomycorrhizal fungi populations decline in *P. cinnamomi* infestations, this may affect tree recovery post-infestation.

There is an increasing volume of literature describing cascading effects of *P. cinnamomi* to local fauna in Australia (e.g., Armistead, 2008; Dundas et al., 2013, 2016; Garkaklis et al., 2004; Laidlaw & Wilson, 2006; Newell & Wilson, 1993; Wilson et al., 1994), and tree declines can impact a range of fauna through removal of habitats and food sources (Fleming et al., 2021). For example, old tree hollows and logs provide important habitat for a wide range of jarrah forest fauna (e.g., Armistead, 2008; Whitford, 2002); however, our results suggest that fewer trees in *P. cinnamomi* infestations may reach the size required to provide these hollows in our study areas (Whitford, 2002).

Implications for supporting tree populations

Continued tree declines may be occurring in other *P. cinnamomi* infestations of the jarrah forest; however, there has been little monitoring of trees in infested systems in the past 20 years since McDougall et al. (2002) who did

not observe recruitment failure. We stress the need for continued monitoring of ecosystem health in *P. cinnamomi* infestations to understand potential long-term effects and to guide management actions. Regular phosphite injections to mature jarrah work to prevent death from the pathogen (Hardy et al., 2001; Jackson et al., 2000). Although, the bottleneck to population growth is largely due to a lack of recruitment success. Hardy et al. (1996) observed successfully established jarrah and marri trees to have high survival in *P. cinnamomi*-infested bauxite rehabilitation after 5 to 7 years. Our findings support this and provide optimism that established trees may have high survivability within infestations.

Planting developed seedlings and supporting their growth may enable them to grow sufficient roots to outlast pathogen impacts and thus survive to grow into established mature trees. For example, restoration of degraded tuart forests has proven successful with the planting of 6-month-old, ~15 cm tall tuart seedlings (Ruthrof et al., 2016), and we suggest planting jarrah or marri of this size also. Additionally, fertilizer tablets can greatly assist tuart seedling growth (Ruthrof et al., 2016) and may also assist survival and growth of jarrah and marri seedlings within *P. cinnamomi* infestations (Stoneman et al., 1995). We also highlight the importance of finding and planting genetically resistant trees in *P. cinnamomi* infestations (Bose et al., 2023; Shearer, 2014; Stukely & Crane, 1994) so that future generations of trees can potentially grow with resistance as a trait (e.g., Stukely & Crane, 1994; Vivas et al., 2021). Broadcasting of seeds may be a successful restoration strategy within infestations as observed on restored mine sites (Colquhoun & Hardy, 2000; Koch & Samsa, 2007); however, annual phosphite applications for the initial 2–3 years of growth may be required to ensure seedling establishment. Assisted recovery of jarrah and marri is likely to be necessary to prevent canopy collapse of *P. cinnamomi*-infested jarrah forest.

AUTHOR CONTRIBUTIONS

Thomas Mansfield: Conceptualization (equal); data curation (lead); formal analysis (lead); investigation (lead); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Giles Hardy:** Conceptualization (equal); funding acquisition (equal); investigation (supporting); methodology (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (equal). **Patricia Fleming:** Conceptualization (equal); formal analysis (supporting); methodology (equal); supervision (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal). **Rachel Standish:** Conceptualization (equal); investigation (supporting); methodology (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code and data are available in Figshare at 10.6084/m9.figshare.24117291.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.