

Climate change or tree disease: challenges for diagnosing causes of forest die-off

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ABSTRACT

Context. Forest ecosystems experience compositional and structural changes as species' environmental envelopes shift with climate change. Extreme climate events and pests/pathogens are driving these ecosystem changes. Determining which of the two potential drivers is causing a particular forest die-off can be challenging. In south-western Australia, widespread forest die-off in 2011 coincided with extremely hot and dry conditions. It occurred in a forest ecosystem that has historically experienced *Phytophthora cinnamomi* root disease (*Phytophthora* dieback). **Aims.** To determine whether the causal agent of *Phytophthora* dieback, *P. cinnamomi*, was associated with forest die-off in the Northern Jarrah Forest. **Methods.** A combination of direct (isolation of pathogen) and indirect (survey of susceptible indicator plant species) measurements were taken inside and outside patches of forest experiencing the die-off. **Key results.** There was no consistent association between die-off patches and the presence of *P. cinnamomi*. *P. cinnamomi* was isolated from 3 of 33 control plots and 3 of 33 die-off plots. Although several plant species susceptible to *P. cinnamomi* were absent from die-off plots, the findings were inconsistent across species. This may be explained by plant tolerance to high temperatures and drought. **Conclusions.** *P. cinnamomi* was not the proximate cause of the observed die-off in the Northern Jarrah Forest in 2011. **Implications.** Novel disturbance caused by extreme climate events can mimic damage caused by certain pests/pathogens. More research is needed to determine the tolerances of plants to extreme temperature and drought conditions to disentangle abiotic and biotic drivers of tree die-off.

Keywords: climate change, drought, eucalypt dieback, *Eucalyptus marginata*, extreme climate event, jarrah, *Phytophthora cinnamomi*, *Phytophthora* dieback.

Introduction

Changes in species' environmental envelopes with climate change are expected to result in compositional, structural and ecosystem-type shifts in the coming decades in many regions (Anadón et al. 2014; Taylor et al. 2017). The direct effects of climate change and the influence of forest pests and pathogens are expected to be the proximate mechanisms driving these shifts (Beckage et al. 2008; Dukes et al. 2009). Therefore, understanding the relative roles of these two mechanisms is vital for determining the rate and direction ecosystems will shift and developing potential mitigation strategies.

Management of *Phytophthora* diseases, which are among the most destructive tree diseases worldwide (Hansen 2015; Burgess et al. 2017), is likely to become increasingly complex because of climate change. Soil-borne *Phytophthora* species rely on soil moisture for movement, reproduction and infection of hosts, making the disease susceptible to climate change-driven moisture changes (La Porta et al. 2008; Sturrock et al. 2011). Whereas some future climate scenarios, including drying, may reduce the severity of *Phytophthora* diseases in certain regions, other regions may experience an increase in severity of the disease due to optimal conditions for the manifestation of the phenomenon (Aguayo et al. 2014; Homet et al. 2019). *Phytophthora* diseases may also interact with climate drivers of tree stress to cause greater tree die-off and mortality (Corcobado et al. 2014). Finally, climate change is likely to result in tree damage that is rarely documented, which has the potential to mimic disease symptoms and lead to misdiagnosis. This effect of

climate change may be particularly important for root disease caused by *Phytophthora* species, because disease diagnosis and mapping are commonly symptom-driven (Hardy *et al.* 2007; Wilson *et al.* 2012), owing to the high costs and frequent false negatives of isolation and culture methods (Hüberli *et al.* 2000).

The Mediterranean climate region of south-western Australia provides a model region to highlight the management challenges and ecosystem effects of climate change and introduced *Phytophthora* pathogens on forest ecosystems. The region has experienced declining precipitation (Timbal *et al.* 2006; Delworth and Zeng 2014) and increasing temperatures in recent decades (Hope *et al.* 2015), resulting in significant declines in streamflow (Liu *et al.* 2019) and groundwater levels (Liu *et al.* 2019; McFarlane *et al.* 2020), among other changes. Most ecosystems have also been affected by the introduction of species of the soil-borne water mold, *Phytophthora* (Shearer *et al.* 2007; Ritchie *et al.* 2021). Corresponding with these climate and disease changes, a wide variety of forest and woodland tree species have experienced episodes of tree die-off, crown decline and tree mortality (Hooper and Sivasithamparam 2005; Dakin *et al.* 2010; Matusick *et al.* 2012, 2013; Paap *et al.* 2017; Wentzel *et al.* 2018; Ritchie *et al.* 2021). *Phytophthora cinnamomi*, one of the most destructive plant pathogens worldwide (Burgess *et al.* 2017; Sena *et al.* 2018), remains the predominant pathogen threat to ecosystems in south-western Australia (Shearer *et al.* 2004, 2007), causing significant dieback. It kills plants throughout the South-West Botanical Province (Shearer *et al.* 2004), including in the *Banksia* woodland ecosystem (Shearer and Dillon 1996), the hyper-diverse Stirling Range (Wills 1993) and the jarrah forest ecosystem (McDougall *et al.* 2002). Understorey plant species, especially those in the Proteaceae, Fabaceae and Ericaceae (among others), are especially susceptible to disease. Since its discovery in the jarrah forest ecosystem, *P. cinnamomi* has been considered the cause of progressive crown dieback, leading to mortality of stands of overstorey jarrah (*Eucalyptus marginata*) trees ('*Phytophthora* dieback'). However, more recently, the direct role of *P. cinnamomi* in the death of jarrah is under debate (Davison 2015, 2018). Regardless of the role of *P. cinnamomi* in jarrah's decline and death, it remains a clear threat to the vegetative biodiversity of the jarrah forest ecosystem. The future sustainable use of the jarrah forest for recreation, conservation and bauxite mining is contingent on the successful management of *P. cinnamomi* (Colquhoun and Hardy 2000).

Mapping the distribution of *P. cinnamomi* is the most critical component of *Phytophthora* dieback management. Various direct and indirect methods have been used to map *P. cinnamomi* in the jarrah forest (Dell *et al.* 2005). Research has increased the accuracy and decreased the cost of detecting the pathogen's presence through direct isolation (Aghighi *et al.* 2016), and *in situ* and *ex situ* baiting using soil and susceptible plant material (Burgess *et al.* 2021). However,

these methods continue to be impractical for mapping large geographic areas or complex patterns of disease distribution and are mostly used strategically to supplement indirect disease mapping methods. The approach most relied on includes using the presence/absence of species known to be susceptible to the disease (Koch 2007). Disease symptoms and pathogen isolation are most common on the 'dieback front' (McDougall *et al.* 2002), and by identifying the presence of symptoms in susceptible species, skilled 'dieback interpreters' develop maps of the leading edge of infested patches. Then, the disease can often be effectively contained by avoiding the movement of infested soil and plant material from infested to not infested areas (Dunstan *et al.* 2010). Therefore, a thorough understanding of the stressors and potential causes of plant symptom development is necessary for accurate *P. cinnamomi* mapping.

In 2011, extensive areas of the Northern Jarrah Forest (NJF) experienced rapid canopy die-off (Fig. 1) associated with extreme climatic conditions, including a heatwave-compounded drought (Matusick *et al.* 2013). The die-off was most common on sites containing rocky soils with low water-holding capacity, at high elevations, on steep slopes surrounding rock outcrops, in xeric areas (Brouwers *et al.* 2013; Andrew *et al.* 2016), with shallow bedrock and thin soils (McGrath *et al.* 2023), and most severe on sites experiencing a long-term precipitation decline (Matusick *et al.* 2018). Forest vegetation surrounding rock outcrops experiences waterlogging during precipitation events, and excessive soil drying during drought (Withers 2000; Schut *et al.* 2014). These soil conditions, including repeated cycles of waterlogging (root hypoxia), are known to stress jarrah directly (Davison and Tay 1985), as well as potentially increase the *P. cinnamomi* infection in jarrah roots (Davison and Tay 1987). Increasing the complexity, one of the largest and most common plant species used for mapping *P. cinnamomi*



Fig. 1. Canopy die-off in the Northern Jarrah Forest of south-western Australia in 2011.

infestation (*Banksia grandis*) experienced widespread die-off during the heatwave-compounded drought event in 2011, exhibiting symptoms similar to those of *P. cinnamomi* infection (Steel et al. 2019). The unprecedented die-off of *B. grandis*, and other species susceptible to *P. cinnamomi*, presented the opportunity for confusion and uncertainty when mapping *Phytophthora* dieback. Whereas the die-off event was strongly associated with extreme climatic conditions, the role of *P. cinnamomi* remains unclear. Thus, this study aimed to determine whether there was a consistent association between *P. cinnamomi* presence and areas of the NJF experiencing die-off in 2011.

Methods

Study area

The Northern Jarrah Forest (NJF) occupies 1.1 million ha on the Darling Plateau, a topographic feature that parallels the western coast approximately 20–30 km inland, with undulating topography ranging from ~200 m to ~300 m above sea level (Fig. 2). Several prominent peaks rise above the plateau (~500–600 m above sea level). Most of the NJF has a lateritic duricrust resulting in surface soils dominated by coarse gravels. The bedrock is granitic, which has led to the formation of a clay

subsoil occupying the space between the duricrust and granite basement (Churchward and Dimmock 1989). Clay depths vary greatly from non-existent surrounding rock outcrops up to 40 m (Dell et al. 1983). There is a slight north–south temperature gradient within the NJF, and a strong west–east precipitation gradient, historically ranging from ~1200 mm year⁻¹ in the west to ~630 mm year⁻¹ in the east (Gentili 1989). Corresponding with the relatively good growing conditions in the west, and poorer conditions in the east, the forest structure is significantly denser and taller in the west than the relatively short, open forest in the east. The NJF has historically been used for timber production (Bradshaw 1999). However, since the 1970s, the forest has increasingly been managed for multiple uses, including bauxite mining, recreation and biodiversity conservation.

P. cinnamomi

The soil-borne water mold, *P. cinnamomi*, was thought to be introduced to south-western Australia prior to 1920. A combination of factors led to the movement and proliferation of the pathogen throughout large portions of the NJF between 1940 and 1970, including a lack of understanding and appreciation for the magnitude of the disease problem and extensive road construction with potentially infested gravel material

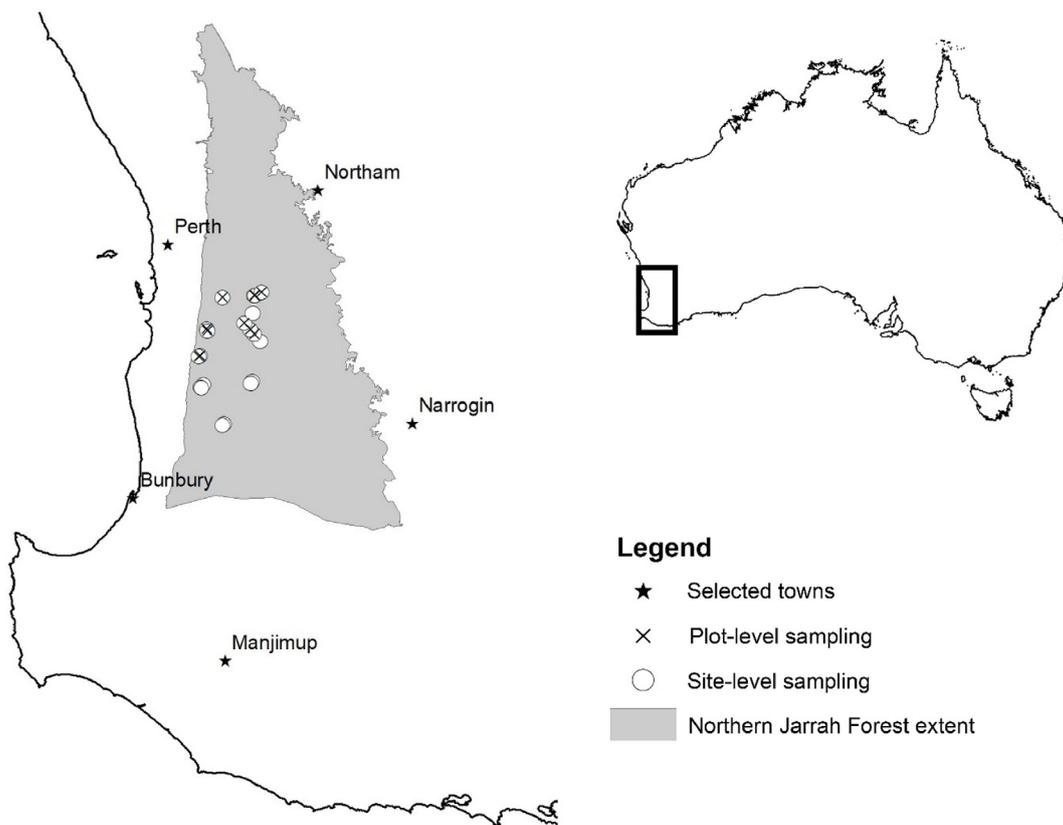


Fig. 2. Map of the Northern Jarrah Forest in south-western Australia, including 20 sites sampled for *Phytophthora cinnamomi* at the site level and 11 sites sampled for *P. cinnamomi* using unbiased baiting and isolation procedures.

(Dell and Malajczuk 1989). Today, *P. cinnamomi* is known to occur throughout the western forest margin and across all topographic positions. Moving inland from the infested escarpment, the disease-affected forest becomes increasingly concentrated in drainage and lower-slope topographic positions, because *P. cinnamomi* moves readily through the movement of soil water (McDougall *et al.* 2002).

Site selection

Shortly following the cessation of the forest die-off event in NJF in 2011, 20 symptomatic areas were selected randomly from a larger sample detected during an aerial survey in May 2011 (see Matusick *et al.* (2013) for details). The boundary of each area affected by die-off, defined as having >70% of trees exhibiting dying or recently killed crowns, was delineated accurately by using a differential GPS. Three points were selected randomly within each die-off patch, representing the centre of a 6-m radius (0.011 ha) circular plot. Because die-off patches were clearly defined, control areas that exhibited minimal crown symptoms could be close to symptomatic ones. Therefore, three control plots were established approximately 20 m from the boundary of the forest experiencing die-off.

Site sampling

Traditionally, the presence and distribution of *P. cinnamomi* have been determined at the site level in advance of timber harvest or other projects involving soil movement. Site-level sampling provides the greatest possible chance of detecting *P. cinnamomi*. For each study site (Fig. 2), including the area within and surrounding die-off patches, the presence of *P. cinnamomi* was evaluated on the basis of the interpreter guidelines (Department of Conservation and Land Management 2001). The guidelines involve assessing the interpretability of the site, detecting and demarcating obvious infested areas and establishing transects through less obvious portions of the site. Samples of symptomatic, susceptible plant species and soil surrounding the plants were collected and baited to detect *P. cinnamomi* (see below for plot sampling methods). The result of the investigation determined whether *P. cinnamomi* was present within or near delineated die-off patches.

Plot sampling

In addition to site-level sampling, study plots were also sampled in 11 of the 20 study sites. Plot-level sampling was more random than site-level sampling and was conducted to directly examine the association between vegetation health and *P. cinnamomi* presence. Each 6-m radius plot was divided into four equal quadrants (north-west, north-east, south-east, south-west). Within each quadrant, two 25 cm × 25 cm × 5 cm soil monoliths were collected. Samples were preferentially taken near symptomatic understorey plants susceptible to *P. cinnamomi* (examples in Table 1).

Phytophthora baiting and isolation

Each soil sample was sifted using a sieve to isolate coarse roots (>2 mm diameter). The sieve was sterilised between the samples each time. A sample of coarse roots and sifted soil was taken from each sample location and bulked for each plot quadrant. This process resulted in four soil samples and four root samples from each plot. Soil and root samples were baited within 2 days of field collection in a baiting container (15 cm long × 5 cm wide × 5 cm deep). *Phytophthora* species baiting followed a protocol developed by the Centre for Phytophthora Science and Management (CPSM), Murdoch University (Burgess *et al.* 2021). Sample material was saturated with distilled water for 24 h, followed by complete flooding. Young *Quercus* spp. (*Quercus suber* and *Quercus ilex*) leaves were floated on each baiting tray following flooding. Baits were checked daily for discoloration and symptoms of infection for 20 days. When symptoms were detected, diseased leaf tissue was cut into sections and plated on *Phytophthora*-selective media (NARPH, Hüberli *et al.* 2000). Representatives of all Pythiaceae colonies were isolated. However, only *P. cinnamomi* was identified to species on the basis of morphological characteristics.

Understorey species survey

The presence of native plant species that are known to be highly susceptible to *P. cinnamomi* in the 6-m study plots suggests that the pathogen may not be present. To examine this indirect evidence for the absence of *P. cinnamomi*, all understorey and mid-storey species were recorded within each of the 120 plots, spanning all 20 die-off patches, in late winter/spring (June–October 2011). Each of the plants was categorised into *P. cinnamomi* susceptibility classes on the basis of McDougall (2005) (Table 2). Here, we report results on 10 common plant taxa that are known to be either highly or moderately susceptible to *P. cinnamomi* infection and mortality (McDougall 2005) (Table 1). A binary logistic regression using SAS software (SAS ver. 9.4, Cary, NC, USA) was implemented to explore the association between plot health (die-off vs control) and presence/health condition of each of the focal 10 species.

Results

By using established site-level interpretation approaches, *P. cinnamomi* was detected at 3 of 20 sites (Table 3). This included one detection within a patch experiencing canopy die-off and three detections outside patches of canopy die-off.

Of the 11 sites where *P. cinnamomi* was assessed at the plot level via isolation, *P. cinnamomi* was detected at four sites. At a plot level, *P. cinnamomi* was found at 3 of 33 plots in control forest, not experiencing die-off, and at 3 of 33 plots in forest experiencing die-off. *P. cinnamomi* was found using both site-level and plot-level methods on one site. In total, including

Table 1. Key understorey and mid-storey species of the Northern Jarrah Forest, south-western Australia, that are susceptible to *Phytophthora cinnamomi* (modified from Groves et al. (2009), McDougall (2005), see references therein).

Species	Susceptibility	Reference/s
<i>Adenanthos barbiger</i>	S, HS	Alcoa of Australia (2002), Shearer and Dillon (1995)
<i>Banksia grandis</i>	S, HS	Alcoa of Australia (2002), Cho (1983), McCredie et al. (1985), Podger (1972), Shearer and Dillon (1996), Shearer and Dillon (1995), Wills (1993), Barrett (1996)
<i>Boronia fastigiata</i>	S	McDougall (1997)
<i>Hibbertia amplexicaulis</i>	S, HS	Shearer and Dillon (1996), McDougall et al. (2002), Edmiston (1989), McDougall (1997), Shearer and Dillon (1995)
<i>Leucopogon capitellatus</i>	S, MS	Alcoa of Australia (2002), Edmiston (1989), Hill (1990), McDougall et al. (2002), Shearer and Dillon (1996), McDougall (1997), Wills (1993)
<i>Leucopogon verticillatus</i>	S, HS	Alcoa of Australia (2002), Edmiston (1989), Shearer and Dillon (1996), Shearer and Dillon (1995), McDougall (1997)
<i>Persoonia elliptica</i>	S, HS	Alcoa of Australia (2002)
<i>Persoonia longifolia</i>	S, HS	Alcoa of Australia (2002), McDougall et al. (2002), Podger (1972), Titze and Palzer (1969), McDougall (1997), Wills (1993), Barrett (1996)
<i>Xanthorrhoea gracilis</i>	S, HS, SP	Alcoa of Australia (2002), Edmiston (1989), Hill (1990), McDougall et al. (2002), Podger (1972), Shearer and Dillon (1996), McDougall (1997), Wills (1993)
<i>Xanthorrhoea preissii</i>	S, HS, SP	Alcoa of Australia (2002), Edmiston (1989), Hill (1990), McDougall et al. (2002), Podger (1972), Shearer and Dillon (1995), McDougall (1997), Wills (1993), Barrett (1996)

S, susceptible; MS, moderately susceptible; HS, highly susceptible; SP, susceptible but persistent.

Table 2. Susceptibility rating to *Phytophthora cinnamomi* (modified from McDougall (2005), see references therein).

Susceptibility rating	Description	References
HS: Highly susceptible	Species highly susceptible, i.e. species that are frequently and consistently killed in the wild, following infection by <i>P. cinnamomi</i> , and/or appear to decline or be rare on infested sites	Includes scale categories 10, 11 and 12 of Wills (1993) and Barrett (1996), and groups 3 and 5 of Shearer and Dillon (1995)
MS: Moderately susceptible or variable susceptibility	Species that are often killed following infection by <i>P. cinnamomi</i> in the wild, but many plants that commonly survive	Includes scale categories 7, 8 and 9 of Wills (1993) and Barrett (1996), and group 4 of Shearer and Dillon (1995)
LS: Low susceptibility	Species that are rarely but occasionally found dead on infested sites	Includes scale categories 4, 5 and 6 of Wills (1993) and Barrett (1996), and group 2 of Shearer and Dillon (1995)
S: Susceptible and thought to be affected	Degree of susceptibility not documented	
SP: Susceptible but persistent	Species that are frequently killed following infection by <i>P. cinnamomi</i> in the wild, but which persist on affected sites through effective reproductive strategies	
SV: Variable susceptibility	Plants may be commonly killed on some infested sites but appear unaffected on others – this may be attributable to genetic differences among populations or differences in site characteristics that influence plant responses	
FR: Field resistant or tolerant	Species that appear to be unaffected by <i>P. cinnamomi</i> in the wild when it is present and for which deaths in the field can rarely be associated with infection by <i>P. cinnamomi</i>	Includes scale categories 1, 2 and 3 of Wills (1993) and Barrett (1996), and group 1 of Shearer and Dillon (1995)
Q: Not known to be directly affected	Rarely found on affected sites (and may be affected either directly through infection or changes in habitat)	

both site- and plot-level methods of detection, *P. cinnamomi* was detected at 6 of the 20 total study sites. There were situations where plot-level sampling detected *P. cinnamomi* and site-level interpretation did not (Sites 80 and 165).

Plot health (die-off vs control) contributed significantly to explaining the presence of 2 of 10 plant species known to be susceptible to *P. cinnamomi* (Table 4). *Adenanthos barbiger* and *B. grandis* were more likely to occur in control plots

Table 3. Twenty research sites in the Northern Jarrah Forest, south-western Australia, within (die-off) and outside (control) patches experiencing die-off following heatwave-compounded drought in 2011.

Site number	<i>Eucalyptus marginata</i> trees (%)		<i>E. marginata</i> trees dying or recently killed (%)		<i>Phytophthora cinnamomi</i> site-level interpretation (1 = positive detection)		Plot-level <i>P. cinnamomi</i> sampling ^A	<i>P. cinnamomi</i> detection (%)	
	Control plots	Die-off plots	Control plots	Die-off plots	Within die-off patch	Outside die-off patch		Control plots	Die-off plots
1	20	85	6	33	0	0	1	0	0
2	80	89	0	0	1	1	1	33	0
5	77	99	0	89	0	0	1	33	0
27	89	79	6	100	0	0	1	0	0
48	71	91	15	90	0	0	1	0	0
59	94	89	0	96	0	0	0		
74	63	95	0	100	0	0	1	0	0
80	78	66	29	33	0	0	1	33	66
87	100	43	0	60	0	0	0		
96	65	99	5	67	0	0	0		
98	60	62	0	92	0	0	0		
99	78	60	0	95	0	0	0		
152	73	86	0	53	0	1	0		
155	41	69	9	49	0	0	0		
165	66	85	3	82	0	0	1	0	33
166	73	92	12	66	0	0	1	0	0
181	49	71	0	100	0	0	1	0	0
183	92	61	11	33	0	0	1	0	0
232	100	95	0	32	0	0	0		
240	77	98	0	88	0	1	0		

All sites had site-level interpretation and a subset of sites (11, with three control and three die-off plots) were assessed for *Phytophthora cinnamomi* by using isolation at the plot level ($n = 8$ sample/plot).

^ASites sampled for *Phytophthora cinnamomi* by isolation from roots and soil denoted as 1.

Table 4. Plant species susceptible to *Phytophthora cinnamomi* and their presence in plots located in control (non-symptomatic) forest and forest experiencing die-off in 2011 in the Northern Jarrah Forest, south-western Australia.

Species	Control plots (%)	Die-off plots (%)	χ^2	P-value
<i>Adenanthos barbiger</i>	45	40	8.3835	0.0038
<i>Banksia grandis</i>	65	25	12.8024	0.0003
<i>Boronia fastigiata</i>	30	10	2.7332	0.0983
<i>Hibbertia amplexicaulis</i>	65	45	0.7078	0.4002
<i>Leucopogon capitellatus</i>	35	30	0.0577	0.8102
<i>Leucopogon verticillatus</i>	30	30	2.1021	0.1471
<i>Persoonia elliptica</i>	10	10	0.6755	0.4111
<i>Persoonia longifolia</i>	80	45	3.6078	0.0575
<i>Xanthorrhoea gracilis</i>	70	55	1.2449	0.2645
<i>Xanthorrhoea preissii</i>	75	90	1.681	0.1948

than in plots experiencing die-off. Other species had similar trends, including *Persoonia longifolia* and *Boronia fastigata*, but plot health was not a significant predictor at $P = 0.05$. Among the sites where *P. cinnamomi* was confirmed present (either by site- or plot-level methods), the 10 susceptible plant species were found on ~50% of control plots and ~28% of die-off plots.

Discussion

There was no evidence of a consistent association between *P. cinnamomi* and forest experiencing die-off, which would be required to attribute the die-off to *P. cinnamomi* infestation. Instead, *P. cinnamomi* was confirmed on a small subset of sites. These findings are unsurprising because *P. cinnamomi* is known to infest sites throughout the NJF (McDougall *et al.* 2002). However, the presence of *Phytophthora* root pathogens

does not automatically imply disease, because specific environmental factors must be aligned with pathogen biology and host susceptibility (Shearer and Crane 2014). From vegetation surveys, there was minimal indirect evidence of the association between *P. cinnamomi* and forest die-off in 2011. Certain plant species susceptible to *P. cinnamomi* were found less frequently on die-off plots. However, this pattern was not consistent across all indicator plant species. We consider the observed differences in plant species between sites to represent weak evidence since these differences may be explained by tolerance to drought and heat, which is largely unknown. For example, *B. grandis*, commonly used for mapping *P. cinnamomi* infestations because of its high susceptibility, appears less tolerant of drought stress than do other mid-storey species in the NJF from field observations (Matusick et al. 2013; Steel et al. 2019). The low frequency of *P. cinnamomi* isolation and inconsistent indirect evidence of *P. cinnamomi* infestation leads us to conclude that *P. cinnamomi* was not consistently associated with the forest die-off patches and was not the primary cause of the die-off event in the NJF.

Uncertainty in the weeks and months following the onset of die-off in the NJF regarding the cause of the damage highlights an understudied challenge climate change is likely to impose on forest managers. Most research regarding the interaction between climate change and biotic pests of forests focuses on shifts in geographic distributions (Bergot et al. 2004; Ikegami and Jenkins 2018), changes in pest biology (Mitton and Ferrenberg 2012) and host resistance (Cudmore et al. 2010). However, tree and forest die-off can be associated with extreme climatic events and biotic sources of tree stress (Shaw et al. 2005; Navarro-Cerrillo et al. 2022), creating a potential source of uncertainty regarding the proximate cause. Indeed, several widespread forest die-off events have led to conflicting reports of the proximate causes of die-off because of the association with both abiotic and biotic tree stressors (Jurskis and Turner 2002; Close et al. 2009; Negrón et al. 2009; de Sampaio e Paiva Camilo-Alves et al. 2013). When both extreme climate stress and *Phytophthora* root diseases are present, the cause of die-off may be particularly difficult to diagnose because *Phytophthora* species can be challenging to isolate consistently from tissues (Tsao 1990; Bowman et al. 2007), and disease may be diagnosed from host symptomology (Spencer 1984; Burgess et al. 2009). Such was the case for the NJF following the die-off in 2011, where climate stress and *P. cinnamomi* were suspected of causing the tree die-off. This research suggests that determining causation on the basis of symptomology alone may no longer be valid in many parts of the NJF under a warming and drying climate.

The unprecedented response of terrestrial and marine organisms to climatic extremes in south-western Australia (Ruthrof et al. 2018) highlights the need for basic research regarding the tolerance of species to extreme temperatures, especially when combined with drought. During and following the heatwave-compounded drought in the NJF, plants were

observed responding in ways that had only ever been associated with *P. cinnamomi* infection, fueling confusion regarding the cause of the stress. Basic understanding of temperature and moisture tolerances is unknown for most species in south-western Australia and other regions experiencing similar climate extremes (Breshears et al. 2021). Filling the knowledge gap in species tolerances to extreme temperatures and moisture regimes will be important for interpreting the causes of novel disturbance in the future (Tesky et al. 2015). Once a library of stress tolerances among predominant plant species in different ecosystems is developed, this information could be compiled and disseminated in extension publications and field guides to assist professionals in discriminating among potential stress agents.

In summary, here we have highlighted one understudied phenomenon likely to occur with greater frequency under continued climate change, the challenge of diagnosing proximate causes of novel disturbances. This problem is expected to be particularly acute when biotic stress agents and abiotic sources of stress are both present prior to die-off, and when *Phytophthora* root pathogens are suspected. In the example reported here, a collection of direct and indirect evidence was analysed to conclude that *P. cinnamomi* was not the proximate cause of the observed die-off in the NJF. South-western Australia can be seen as a climate-change hotspot (Andrich and Imberger 2013; Foster et al. 2014), experiencing extreme effects of climate change, and can therefore highlight the novel challenges imposed by a shifting climate.

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