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Quantifying the distribution and threat of *Phytophthora cinnamomi* in New South Wales: implications for its management in natural vegetation

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Abstract: *Phytophthora cinnamomi* is an oomycete (water mould) with a large host range. It infects plants through their roots and in some cases will kill them. The pathogen is readily dispersed in soil and water, over short distances by its swimming spores and over large distances by humans. While *Phytophthora cinnamomi* has been well-studied in other parts of Australia, its distribution and impact are poorly known in New South Wales (NSW). In the current study we compiled existing data on *Phytophthora cinnamomi* occurrence and filled spatial gaps in sampling. We found about 1000 records of *Phytophthora cinnamomi* presence in over 5000 tests of soil and root material, and collected a further 457 samples from areas where no sampling had previously been done. The resulting data set enabled modelling of *Phytophthora cinnamomi* habitat suitability using the software program MaxEnt with climate and soil spatial layers. We found that coastal areas and adjacent tablelands were most suitable for the pathogen, although some areas within that may be unsuitable because of soil properties. We then modelled assets (threatened species) potentially affected by *Phytophthora cinnamomi* to produce a layer of risk. Using projected climate layers, we found that habitat suitability and risk will decline in parts of northern NSW by 2070 but be amplified in the south. New susceptible species in places such as the Australian Alps are likely to be exposed to the pathogen in the future. We offer advice for managing *Phytophthora cinnamomi* in NSW. Management is difficult where the effects of this pathogen are often inconspicuous and its distribution is widespread. However, basic hygiene to limit spread to susceptible assets will have great benefit regardless.

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Introduction

Phytophthora cinnamomi is an oomycete (water mould), which is thought to have originated in south-east Asia (Dobrowolski et al. 2003), although there is evidence for one strain having an Australasian origin (Arentz 2017). It can now be found in all continents (except Antarctica) where it has a range of economic and environmental impacts (Cahill et al. 2008). Hosts of economic importance include avocado, chestnut, grapes, pineapple and commercial forestry species (Cahill et al. 2008). The pathogen can also have catastrophic effects in native vegetation (e.g. in oak forests of Europe (Jung et al. 2013b) and heathlands in South Africa (Von Broembsen & Kruger 1985)) but has had the most dramatic effect in southern Western Australia (Shearer et al. 2007). As a consequence, it is regarded as one of the 100 world's worst invasive alien species in the Global Invasive Species Database (Lowe et al. 2000), and has been listed as a key threat to biodiversity in several Australian jurisdictions.

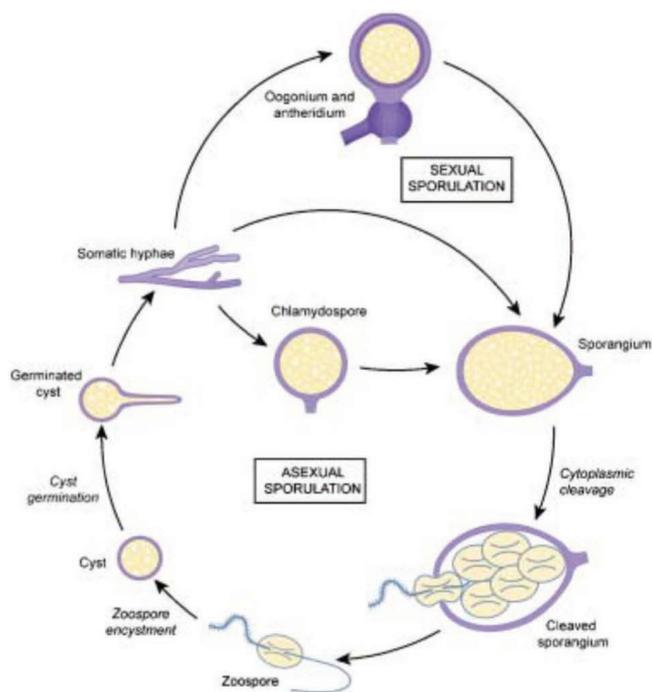


Fig. 1. Life cycle of *Phytophthora cinnamomi*. Reproduced with permission from Hardham (2005).

Phytophthora cinnamomi colonises plants through roots or plant collars. It is a necrotroph, feeding on live cells and often killing plant hosts, rather than a saprophyte, which feeds on plant material that is already dead. Its life cycle involves a range of stages and spore types (Hardham 2018; Fig. 1). In its vegetative stage, mycelial strands spread in its host, damaging the plant's water and nutrient conducting tissues. For that reason, plant death often mimics the effects of severe drought. Mycelial strands may also spread from host to host through contact between roots. Under moist conditions, short-lived motile zoospores are produced from sporangia on the mycelia, which enable dispersal to nearby hosts. Other spore types may be produced under certain conditions. One

of these, the chlamydospore, is relatively long-lived and durable, enabling the pathogen to survive prolonged dry periods (Jung et al. 2013a). Chlamydospores can germinate to produce mycelia and sporangia and ultimately, more zoospores (McCarren et al. 2005). The sexual part of the life cycle leading to the production of oospores requires the presence of the two mating types, A1 and A2. The A1 strain is rare in Australia (e.g. Weste and Marks 1987) and sexual reproduction, if it occurs, is also rare. *Phytophthora cinnamomi* is effectively asexual in Australia.

Phytophthora cinnamomi spreads in soil and water but, importantly, is not airborne. It may spread over short distances from one root to another by motile zoospores or by the growth of mycelium on closely contacting roots (i.e. cm to a few metres; e.g. Hill et al. 1994). However, the pathogen may move longer distances within a site in run-off after storm events (i.e. 100s of metres; Kinal et al. 1993) or when moved by animals in infested soil (i.e. many km; Cahill et al. 2008). Soil may be spread by non-human animals on hooves and even in faeces (Li et al. 2014) but this will typically be on the scale of home ranges (usually a few to several km²). Humans, however, tend to spread it furthest because they can travel much longer distances than non-human animals (e.g. in cars, with heavy machinery, on bikes and horses, or when bushwalking). The relative importance of different dispersal vectors has not been quantified but humans are likely to be the most significant dispersal agents for conservation management because they can rapidly spread it over vast distances and across natural dispersal barriers (e.g. mountain ranges). In the absence of hygiene measures, the likelihood and magnitude of spread by dispersal vectors can be thought of in terms of the quantity of soil that can be dispersed, the distance it can be dispersed and the frequency of dispersal (e.g. a bulldozer carries greater risk of spread than a kangaroo or goat). Once *Phytophthora cinnamomi* is introduced to a new area it is practically impossible to eradicate (Dunstan et al. 2010).

The host range of *Phytophthora cinnamomi* is huge globally (Zentmyer 1980) and in Australia (O'Gara et al. 2006). Some species will be unaffected in the presence of the pathogen or asymptomatic (Phillips & Weste 1984; Crone et al. 2013), while others are highly susceptible under most conditions. Several common Australian plant families have large numbers of susceptible hosts (e.g. Ericaceae, Proteaceae). Loss of dominant species to infection by *Phytophthora cinnamomi* may result in major vegetation change with adverse effects on other elements of ecosystems. Several animal species, for instance, are indirectly at risk because of habitat change and loss of food plants (e.g. the honey possum, Dundas et al. 2016). Diverse heathy woodlands in Victoria have been transformed into communities dominated by tolerant grasses and sedges (e.g. Weste et al. 2002). Some species are being pushed towards extinction because of this pathogen. In the current threat abatement plan for *Phytophthora cinnamomi*, 121 threatened plant taxa are reported to be susceptible to infection (Department of Environment and Energy 2018).

The expression of disease requires three elements: presence of the pathogen, presence of a host and suitable conditions for colonisation and disease development. Suitable conditions are not simply a function of the average (prevailing) climate at any site. Stress is likely to play a major role in disease expression. Climate extremes (e.g. drought, flooding) and the co-occurrence of other pathogens and insect pests may place normally tolerant species at risk. This will become especially important as climate changes. Substantial variation in the pathogenicity of isolates of *Phytophthora cinnamomi* has also been reported (Dudzinski et al. 1993) and so it is possible that the pathogen may have differing impacts across the range of a single vegetation type or susceptible species. Predicting disease where disease expression is stochastic and pathogenicity is variable can therefore be extremely challenging, making management problematic. In addition, some areas where disease is predicted based on climate and the presence of hosts may not be affected because of soil properties. For instance, *Phytophthora cinnamomi* is known to have poor survival and minimal impact in highly organic soils (Halsall 1982) and those with high levels of calcium (Broadbent and Baker 1974, Trochoulias et al. 1986). Soil microbes are also likely to be important in suppression of *Phytophthora cinnamomi* activity (Broadbent and Baker 1974, Halsall 1982).

The impact of *Phytophthora cinnamomi* in New South Wales (NSW) is often much less obvious than it is in southern States (especially Western Australia (WA)). There are major differences in the susceptibility of some host genera. *Banksia* species in WA, for instance, have been assessed in a field trial as being of moderate to high susceptibility while NSW *Banksia* species are generally of low susceptibility (McCredie et al. 1985). The typically low susceptibility of species in NSW unsurprisingly led to the proposition that the pathogen is native there (Pratt & Heather 1973) and that local plants had adapted to it. An assessment of *Phytophthora cinnamomi* effects in 2001 (McDougall & Summerell 2003b) identified some areas and species in NSW that are especially sensitive to *Phytophthora cinnamomi*, and questioned its native status. At that stage it was evaluated as a widespread pathogen with localised effects; however, large gaps in knowledge were identified. One of the key reasons for *Phytophthora cinnamomi* not being regarded as a pathogen causing severe dieback in NSW is perhaps that its effects are seen mostly in heathlands or in forest understorey rather than in forest canopies (McDougall & Summerell 2003b; McDougall 2005). While many NSW eucalypts are susceptible to infection (see for example Table 6 below), there is no evidence of broadscale eucalypt dieback in NSW native forests caused by *Phytophthora cinnamomi*.

In recent years, other *Phytophthora* species have been detected in NSW and some are having negative effects on native vegetation. One such species is *Phytophthora gregata*, which appears to be pushing the native shrub *Pimelea bracteata* towards extinction in subalpine wetlands (McDougall et al. 2018). This pathogen has been postulated as being native (Burgess et al. 2017b) because it is newly described and until recently largely known from native

vegetation in WA. The origin of such *Phytophthora* species could be investigated genetically but, without adequate resources, most will remain as being of uncertain origin. With climate and land use change, and the likely movement of native and non-native pathogens to new areas, the origin of these species is perhaps irrelevant. If they are affecting ecosystems in a unidirectional way, their effects are worth taking seriously. At least the A2 strain of *Phytophthora cinnamomi* is likely to be non-native in New South Wales; this strain is the more common and is responsible for most damage. In the current paper we have little regard for the origin of *Phytophthora cinnamomi* but focus on its impacts and the consequent needs of conservation management. In addition, the future distribution of *Phytophthora cinnamomi* is likely to change as climate changes, and its climate related movement will occur more quickly than that of its hosts. New vascular plant species are likely to be affected while others may be released from its effects. Greater stress on plants from extreme and changing conditions could also make some species vulnerable where they were apparently tolerant in the past.

The current paper aims to evaluate the distribution of *Phytophthora cinnamomi* in NSW by filling spatial sampling gaps and modelling its current and future distribution against the likely risk to plant species. Species distribution modelling might enable managers to strategically allocate resources to *Phytophthora cinnamomi* management now and plan for the future. But how should managers respond to the threat from this pathogen when it is present? Much of the current management paradigm has come from the Western Australian experience where the distribution of the pathogen is reasonably clear from its visual impact; clean on entry and exit works when you know where the pathogen is and there are plenty of unaffected areas. But will that work in NSW where the pathogen is widespread and the disease status of most vegetation is uncertain, and where much of the vegetation is apparently unaffected even when *Phytophthora cinnamomi* is present? We also aim to provide practical advice to land managers about *Phytophthora* management.

Methods

Existing data

Records of *Phytophthora cinnamomi* presence and absence in NSW and the Australian Capital Territory were obtained from available databases, personal records and published surveys (Table 1). Absence records represent places where the pathogen was tested for but not detected in soil or plant samples. In order to reduce edge effects in species distribution models (especially where using projected climate data for which future climates may not be represented in NSW), data from southern Queensland and northern Victoria were also obtained from the Atlas of Living Australia (<https://www.ala.org.au/>; accessed 26 February 2018).

Table 1. Sources of presence / absence data for *Phytophthora cinnamomi* used for modelling habitat suitability.

Area covered	Time span	Records	Data owner/source
Australian Alps Walking Track	2014-2015	70	Australian Alps National Parks Co-operative Management Program
Kosciuszko National Park	2016-2017	57	Ihsanul Khaliq / Murdoch University
Eastern NSW	1999-2019	232	Department of Planning, Industry and Environment unpublished data
Greater Blue Mountains World Heritage Area	2010 - 2011	2129	Newby (2014)
Hawkesbury Nepean Catchment Management Authority area	2007 - 2008	405	Suddaby & Liew (2008a)
NSW (northern) and QLD (southern) Gondwana Rainforests of eastern Australia	2011 - 2012	1303	Bishop <i>et al.</i> (2012), Scarlett <i>et al.</i> (2015)
NSW State Forests	2019	56	Angus Carnegie / Forestry Corporation of NSW
NSW, Queensland and Victoria	1965-2017	604	Atlas of Living Australia (http://www.ala.org.au/ ; accessed 26 Feb 2018)
Royal National Park	2001-2002	35	Keith <i>et al.</i> (2012)
Sydney Metropolitan Catchment Management Authority area	2005-2008	470	Suddaby & Liew (2008b)

Duplicate records were removed and others checked for spatial accuracy by comparing location descriptions with their location on ArcMap 10.4; those with unresolvable location issues were also removed. The resulting data set contained 5205 records - *Phytophthora cinnamomi* was present in 1061 of these. A further 56 sample results, of which 19 were positive for *Phytophthora cinnamomi*, became available after the modelling component of the project was completed. These were included only for testing environmental correlates of *Phytophthora cinnamomi* presence.

Additional sampling

Additional soil sampling for the presence of *Phytophthora cinnamomi* was conducted between August 2018 and April 2019 to fill spatial sampling gaps and extend sampling to the semi-arid zone (above about 350 mm annual rainfall) where few samples had previously been taken in NSW. The State was first divided into 1' grids and the number of samples required per grid to address spatial gaps was apportioned according to the available budget and the likelihood of detection (with fewer samples identified with increasing distance from the coast, reflecting knowledge of

Phytophthora cinnamomi distribution elsewhere). Sample sites were chosen before the survey using vegetation layers on ArcMap 10.4, in a range of habitats but preferably in areas likely to be suitable (e.g. disturbed roadside vegetation, swamp edges). This was especially important in semi-arid areas, which were in drought at the time of survey.

At each sampling site, about 400 g of soil and roots was collected in total from under plants in four places within the site using a trowel. The samples were sealed in ziplock bags and labelled with the site number. The bags were sent to the Royal Botanic Gardens Sydney for testing as soon as possible after collection. In total, 457 new samples were collected and tested for the presence of *Phytophthora cinnamomi* (and other *Phytophthora* species).

Phytophthora detection

A baiting system of blue lupins (*Lupinus angustifolius*) was used to detect *Phytophthora*. Soils and roots from each sample were mixed in a zip-lock plastic bag and flooded with de-ionized water. Pre-germinated lupins were suspended above the soil-water slurry and incubated for 7 days at 22°C. For *Phytophthora* identification, total DNA extraction from the lupin radicles was conducted followed by polymer chain reaction (PCR) with *Phytophthora* specific primers developed by Schena *et al.* (2008) that targeted the ras-related protein (Ypt1) gene region. Total DNA was extracted from the distal 10 mm of the lupin radicles using the FastDNA Kit (Q-biogene Inc., Irvine, California, USA) according to the manufacturer's instructions. Species identification was initially based on *Phytophthora* specific PCR (Schena *et al.* 2008), but where species identification was unclear, especially for non-*Phytophthora cinnamomi*, sequencing of the nuclear ribosomal DNA, internal transcribed spacer 1 and 2 (ITS) and BLAST analysis in NCBI's GenBank were carried out. The ITS and Ypt1 were amplified using primer sets and PCR conditions described in Cooke *et al.* (2000) and Schena *et al.* (2008), respectively. Amplicons were purified using ExoSAP-IT (USB Corporation Cleveland, Ohio, USA) according to the manufacturer's instructions and sent to the Ramaciotti Centre for Gene Function Analysis at the University of NSW where DNA sequences were determined using an ABI PRISM 3700 DNA Analyser (Applied Biosystems Inc., Foster City, California, USA).

Data limitations and cleaning

The choice of modelling approach was constrained because absence data were not available for Queensland and Victoria. In addition, absence records were only available in NSW for dedicated *Phytophthora* surveys – the location of samples that record negative results are generally not retained. Importantly, absence records for an introduced and cryptic species such as *Phytophthora cinnamomi* are ambiguous. They may mean that the habitat is unsuitable or that the species was present but not detected in the sample. For this reason, presence records only were used for modelling but absence and presence records were used to define the area for modelling. The species distribution modelling program

MaxEnt (Phillips et al. 2006) was used because it does not require absence records.

The data obtained from external sources had been collected for two main reasons: 1) dedicated surveys of *Phytophthora cinnamomi* distribution within defined areas – e.g. Suddaby & Liew (2008a), Scarlett *et al.* (2015); 2) identifying the cause of poor plant health. The second sampling motive probably has a much greater likelihood of detecting the pathogen because it tests soils where there are symptomatic plants. In addition, a large proportion of the samples came from dedicated surveys on the Central Tablelands (especially the Blue Mountains region). The distribution of samples is therefore spatially biased and not uniform in likelihood of detection (Fig. 2), a severe constraint for species distribution modelling (Kramer-Schadt et al. 2013, Fourcade et al. 2014). Spatial bias was reduced by randomly selecting one presence sample from grids measuring 10 x 10 km (see Appendix 1 for the rationale behind the use of this approach).

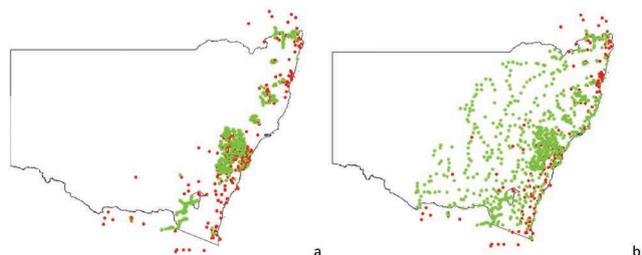


Fig. 2. Location of records of *Phytophthora cinnamomi* in NSW, northern Victoria and southern Queensland used for modelling in this paper, a) recorded prior to the current study; b) including those sampled in the current study to fill spatial gaps; red dots = presence records; green dots = absence records.

Species distribution and risk models

1) *Phytophthora cinnamomi* habitat suitability

Species distribution modelling was performed with the program MaxEnt (Phillips et al. 2006), which creates a probability distribution that maximises entropy (unpredictability) for presence data based on constraints (in this case, environmental variables). MaxEnt uses presence only data and generates background data to test the model output. The output is a GIS raster file with each cell being assigned a value between 0 and 1, 1 being most suitable habitat.

Available environmental spatial layers were assembled, each with a resolution of 1 km², meeting a requirement of MaxEnt for layers to have the same extent and resolution: Climate: 19 Bioclim variables from Worldclim version 1.4 (Hijmans et al. 2005) for the period 1960 – 1990, and three projected climate models from the CGIAR Research Program on Climate Change, Agriculture and Food Security (<http://www.ccafs-climate.org/>; accessed 3 May 2017, Ramirez & Jarvis 2008) for 2070 conditions under two representative concentration pathways (4.5, a moderate scenario where the CO₂ concentration stabilises in the middle of the 21st Century and 8.5, an extreme scenario where CO₂ concentrations rise exponentially); Australian national map layers for physical properties (elevation, geology, soil type, soil water holding

capacity; <https://www.agriculture.gov.au/abares/aclump/multi-criteria-analysis/australian-national-map-layers>, accessed 23 July 2019). The climate projection models used (i.e. ACCESS1-0, CESM1-CAM5, HadGEM2-CC) had above average skill scores for rainfall, temperature, and the southern and eastern regions of Australia (CSIRO & Bureau of Meteorology (2015), which were relevant properties of the current study.

A preliminary model using MaxEnt and including all variables showed that many variables contributed little to the model either when present or absent, and so these were removed. Collinearity of the remaining variables was checked – Bio18 (precipitation of the warmest quarter) was highly correlated with Bio12 (annual precipitation) and was not used in the modelling. None of the other variables had a correlation coefficient (r) > 0.7 and so all were retained: bioclim variables 1 (mean annual temperature), 3 (isothermality = (monthly temperature range ÷ annual temperature range) * 100), 5 (maximum temperature of warmest month), 7 (temperature annual range (Bio5-Bio6)), 8 (mean temperature of wettest quarter), 9 (mean temperature of driest quarter), 12 (annual precipitation), 14 (precipitation of driest month), 19 (precipitation of coldest quarter), Australian Soil Classification. The default settings of MaxEnt were used.

2) Susceptibility and distribution of assets at risk

Phytophthora cinnamomi may affect many values directly (e.g. death of species, degradation of vegetation) or indirectly (e.g. loss of habitat for fauna, economic effect of loss of tourism opportunities with track closures etc.). Modelling the distribution and intensity of all of these was beyond the scope of this project. We chose to focus on the distribution of threatened plant species as these are already regarded as being at risk (often for multiple reasons including rarity) and infection by *Phytophthora cinnamomi* could increase the risk of extinction.

Records of NSW threatened plant species were obtained from Bionet (<http://www.bionet.nsw.gov.au/>; accessed 16 May 2019). All records prior to 1990 were first removed so that the data were more likely to represent extant populations. Duplicates were then removed and geolocation checked against location descriptions using ArcMap 10.4. Data for each species were cleaned and bias reduced using the method described in Appendix 1, and then combined into a single file. Location data were weighted by the likelihood of susceptibility to *Phytophthora cinnamomi* (1 = species with no known congeneric susceptibility, 2 = with known congeneric susceptibility, 3 = species known to be susceptible) multiplied by the threatened status of the species (1 = vulnerable, 2 = endangered, 3 = critically endangered). The distribution of threatened species was modelled using MaxEnt. Variables with low explanatory power and collinearity (r) > 0.7 were first removed, leaving Bio 3 (isothermality), Bio5 (max temperature of warmest month), Bio6 (min temperature of coldest month), Bio8 (mean temperature of wettest quarter), Bio9 (mean temperature of driest quarter), Bio18 (precipitation of warmest quarter), Bio19 (precipitation of coldest quarter) and Australian Soil Classification. Layers for assets were not projected for climate because of expected lag effects for changes in

distribution of vascular plants. In addition, projected models would be required for all susceptible species and combining them into a single layer would multiply the uncertainties of each, producing a model of questionable value.

The broader susceptibility of plant species occurring in NSW was evaluated by compiling available data on isolation of *Phytophthora cinnamomi* from wild, cultivated or glasshouse populations.

3) Risk

Risk from *Phytophthora cinnamomi* is a function of the distribution of the pathogen and the environmental, cultural or economic assets it affects. If *Phytophthora cinnamomi* is likely to be present in an area but no assets are present in that area, the current risk will be low. Similarly, if *Phytophthora cinnamomi* is unlikely to be present in an area and many assets are present in that area, the current risk will be low. Accordingly, risk was assessed as the product of habitat suitability for *Phytophthora cinnamomi* and the likely occurrence of threatened species that may be affected by the pathogen. A risk layer was created in ArcMap 10.4 by multiplying raster values of the *Phytophthora cinnamomi* and asset layers. The risk in 2070 was assessed using 2070 distribution models for *Phytophthora cinnamomi* and the current layer for assets.

Environmental correlates of Phytophthora cinnamomi presence

Environmental variables associated with *Phytophthora cinnamomi* presence were evaluated in randomisation and chi-square tests. The contribution of the variables used in the species distribution model to the overall performance of the model was assessed in MaxEnt (Phillips et al. 2006) for each variable with a jackknife randomisation test of regularised training gain, which is a measure of how well the model fits presence records. Jackknife tests were performed with the bias-reduced presence data used for the species distribution models. The significance of differences in frequency of occurrence for vegetation types and geological types was assessed using chi-square tests comparing observed and expected frequencies of both presence and absence records for each vegetation or geological type.

Results

Of the 457 new samples taken, 395 (87%) tested negative to *Phytophthora* species, 47 (10%) tested positive to *Phytophthora cinnamomi*, while 15 (3%) tested positive to other *Phytophthora* species (Table 2). Most new presence records were from coastal and tableland areas, consistent with previous sampling (Fig. 3). The most western new presence record was from disturbed *Callitris glaucophylla* woodland north of Condobolin (Fig. 4).

Table 2. *Phytophthora* species other than *Phytophthora cinnamomi* identified in new samples collected for the current study.

Species	Samples	IBRA sub-regions
<i>Phytophthora cryptogea</i>	10	Coffs Coast and Escarpment (2 samples), Hill End, Inland Slopes, Kybean-Gourock, Monaro (2), Pilliga, South East Coastal Ranges, Tomalla
<i>Phytophthora</i> sp.	1	Severn River Volcanics
<i>Phytophthora megasperma</i>	1	Inland Slopes
<i>Phytophthora frigida</i>	1	Wyong
<i>Phytophthora multivora</i>	1	Inland Slopes
<i>Phytophthora sansomeana</i>	1	Murrumbateman

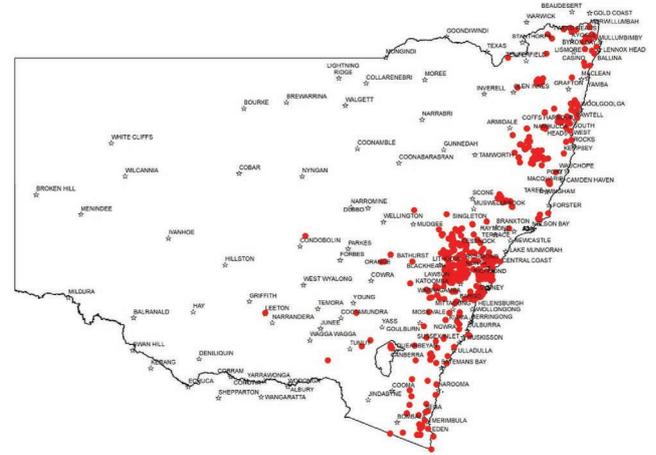


Fig. 3. *Phytophthora cinnamomi* presence records in NSW (to May 2020).



Fig. 4. Disturbed roadside remnant of *Callitris glaucophylla* woodland north of Condobolin, annual rainfall c. 520 mm. The soil sample from this site tested positive for *Phytophthora cinnamomi*.

Environmental correlates of Phytophthora cinnamomi presence

In the species distribution model, annual temperature range (Bio7) was the most important variable by itself. Annual precipitation (Bio12) and mean maximum temperature of the warmest month (Bio5) were almost as important alone but mean annual temperature (Bio1) contributed little to the model. The habitat suitability of *Phytophthora cinnamomi* increased with increasing annual precipitation (Bio12) and decreased with increasing annual temperature range (Bio7); habitat suitability was greatest when the mean maximum temperature of the warmest month was between 21 and 29°C

(Bio5) (Fig. 5). Isothermality (Bio3) had the most effect on the model when removed (Fig. 6).

Phytophthora cinnamomi was found on sites from sea level to 1558 m above sea level, and under a broad range of climatic conditions (Table 3). It was not recorded in arid parts of NSW (typically occurring in areas with annual precipitation above 600 mm) nor in high mountain areas with a mean annual temperature below 9°C. Despite that, it was recorded in areas that are periodically dry (with mean precipitation of the driest month as low as 24 mm) and cold (with mean temperature of the driest quarter as low as 3.9°C).

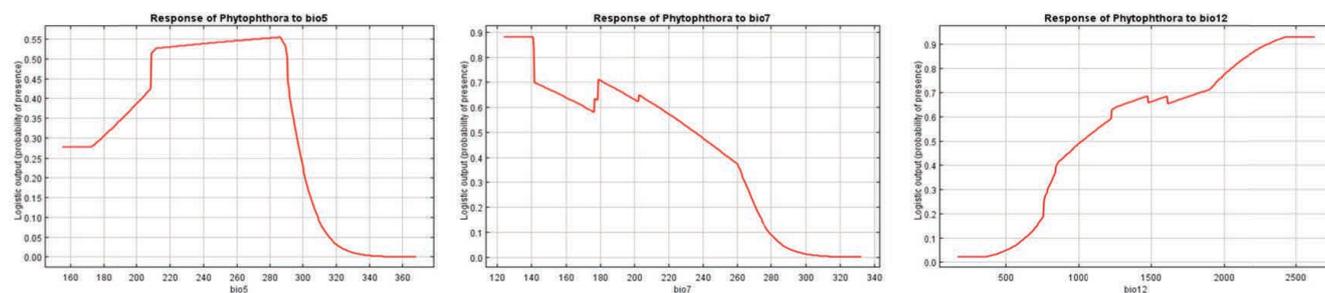


Fig. 5. Response curves of the most important variables in the model of suitability for *Phytophthora cinnamomi* (Bio5 = maximum temperature of warmest month, Bio7 = temperature annual range, Bio12 = annual precipitation). Note that for Bio5 and Bio7, temperature values on the x axis are multiplied by 10.

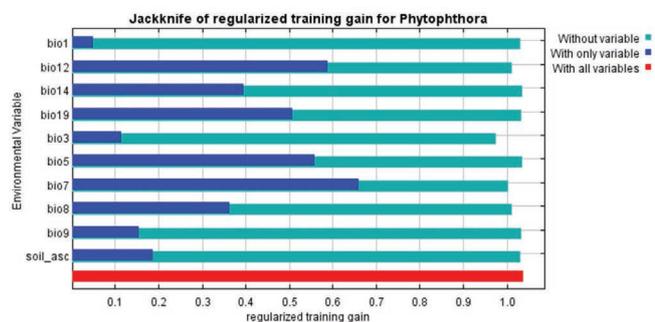


Fig. 6. Jackknife plots of variables included in the species distribution model created using MaxEnt. The red bar indicates the regularized training gain (i.e. how well the model predicts the presence data) from using all variables. The blue bars indicate the amount of training gain for each environmental variable alone while the green bars indicate the training gain when each environmental variable is omitted.

Table 3. Minimum, maximum and 95 percentile values for the climate variables used in the model, and elevation.

Variable	Min	2.5 percentile	97.5 percentile	Max
Bio1: mean annual temperature (°C)	9.0	10.3	20.3	21.7
Bio3: isothermality (mean diurnal range / annual range)	4.3	4.5	5.2	5.2
Bio5: maximum temperature of warmest month (°C)	20.8	22.1	30.6	32.7

Variable	Min	2.5 percentile	97.5 percentile	Max
Bio7: temperature annual range (°C)	14.1	17.9	27.9	30.1
Bio8: mean temperature of wettest quarter (°C)	5.7	8.7	24.3	25.2
Bio9: mean temperature of driest quarter (°C)	3.9	5.6	20.7	22.4
Bio12: annual precipitation (mm)	410	619	1871	2423
Bio14: precipitation of driest month (mm)	24	31	74	85
Bio19: precipitation of coldest quarter (mm)	100	123	351	431
Elevation (m)	1	5	1167	1558

Phytophthora cinnamomi was significantly more likely than random to be found on sites with the following attributes (Tables 4 and 5): **geology**– sandstone ($P < 0.001$); **vegetation** – Cleared ($P < 0.001$), Northern Warm Temperate Rainforests ($P < 0.05$), Southern Lowland Wet Sclerophyll Forests ($P < 0.05$), Sydney Coastal Dry Sclerophyll Forests ($P < 0.01$), Sydney Montane Heaths ($P < 0.05$). It was significantly less likely to be found on sites with the following attributes: **geology** – unconsolidated sediments ($P < 0.001$); **vegetation** - Central Gorge Dry Sclerophyll Forests ($P < 0.05$), North-west Slopes Dry Sclerophyll Woodlands ($P < 0.05$), Western Slopes Dry Sclerophyll Forests ($P < 0.05$). Unconsolidated sediments occur mostly in the west of the study area.

Table 4. Numbers of negative and positive records of *Phytophthora cinnamomi* according to geology with 10 or more samples, the difference between the expected and observed number of positives, and the significance of the difference based on chi-square tests; * P < 0.001.**

Geology	Negative	Positive	Exp - Obs	P
Argillite/Chert	14	9	3	
Basalt	61	23	1	
Claystone	9	2	-1	
Coal	15	0	-4	
Conglomerate	27	13	3	
Granite	60	12	-7	
Granodiorite	37	8	-4	
Greywacke	18	12	4	
Ignimbrite	13	5	0	
Mudstone	12	8	3	
Other Meta-sediments	7	3	0	
Porphyry	10	2	-1	
Quartzite	13	4	0	
Rhyolite	23	9	1	
Sandstone	284	146	33	***
Shale	48	15	-1	
Siltstone	34	13	1	
Unconsolidated Sediments	161	21	-27	***

Table 5. Numbers of negative and positive records of *Phytophthora cinnamomi* according to vegetation type with 10 or more samples, the difference between the expected and observed number of positives, and the significance of the difference based on chi-square tests; * P < 0.05, ** P < 0.01, * P < 0.001.**

Vegetation Type	Negative	Positive	Exp - Obs	P
Alpine Herbfields	12	0	-3	
Central Gorge Dry Sclerophyll Forests	36	4	-6	*
Cleared	150	87	26	***
Coastal Floodplain Forests	11	1	-2	
Coastal Heath Swamps	13	6	1	
Cool Temperate Rainforests	16	6	1	
Eastern Riverine Forests	22	3	-3	
Floodplain Transition Woodlands	20	0	-5	
Inland Riverine Forests	21	0	-5	
Montane Bogs and Fens	12	8	3	
New England Dry Sclerophyll Forests	9	2	-1	
North Coast Wet Sclerophyll Forests	52	27	7	
Northern Escarpment Dry Sclerophyll Forests	5	5	3	
Northern Escarpment Wet Sclerophyll Forests	24	11	2	
Northern Gorge Dry Sclerophyll Forests	14	6	1	
Northern Hinterland Wet Sclerophyll Forests	35	11	0	
Northern Tableland Dry Sclerophyll Forests	22	6	-1	

Vegetation Type	Negative	Positive	Exp - Obs	P
Northern Tableland Wet Sclerophyll Forests	31	14	3	
Northern Warm Temperate Rainforests	22	15	6	*
North-west Floodplain Woodlands	13	0	-3	
North-west Slopes Dry Sclerophyll Woodlands	24	1	-5	*
South Coast Wet Sclerophyll Forests	6	6	3	
South East Dry Sclerophyll Forests	19	8	1	
Southern Escarpment Wet Sclerophyll Forests	7	5	2	
Southern Lowland Wet Sclerophyll Forests	4	6	3	*
Southern Tableland Dry Sclerophyll Forests	28	5	-4	
Southern Tableland Grassy Woodlands	11	0	-3	
Southern Tableland Wet Sclerophyll Forests	26	6	-2	
Subalpine Woodlands	28	8	-1	
Subtropical Rainforests	23	10	2	
Sydney Coastal Dry Sclerophyll Forests	44	30	12	**
Sydney Coastal Heaths	7	6	3	
Sydney Hinterland Dry Sclerophyll Forests	104	49	11	
Sydney Montane Dry Sclerophyll Forests	22	14	5	
Sydney Montane Heaths	15	12	5	*
Sydney Sand Flats Dry Sclerophyll Forests	9	2	-1	
Tableland Clay Grassy Woodlands	8	3	0	
Upper Riverina Dry Sclerophyll Forests	11	1	-2	
Western Peneplain Woodlands	17	0	-4	
Western Slopes Dry Sclerophyll Forests	35	3	-7	*
Western Slopes Grassy Woodlands	24	0	-6	

Species distribution and risk models

1) *Phytophthora cinnamomi* habitat suitability

a) Current suitability

The MaxEnt model of habitat suitability for *Phytophthora cinnamomi* performed well, with an area under the curve (AUC) for training data of 0.883 – the AUC of a random prediction would be 0.5. Habitat for *Phytophthora cinnamomi* (based on climate and soil type) is currently most suitable along the coast and central tablelands (Fig. 7). Suitability generally declines from east to west and is very low on the western slopes and plains.

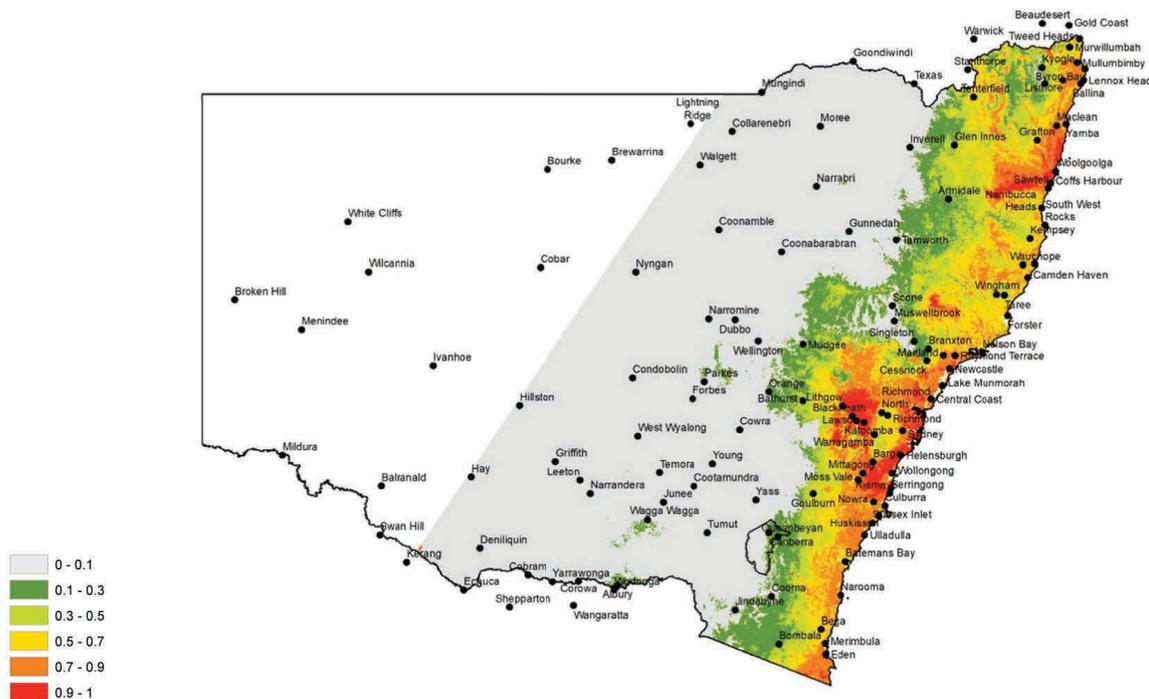


Fig. 7. Current habitat suitability for *Phytophthora cinnamomi* (ranked from 0 = unsuitable to 1 most suitable). The unshaded area was not assessed in the model as there were no presence or absence data there.

b) Future suitability

By 2070 under both climate scenarios (Figs. 8 and 9), habitat suitability for *Phytophthora cinnamomi* will increase along parts of the South Coast and the Southern and Central Tablelands. Northern agricultural areas between Lismore and Tenterfield will become much less suitable. The

representative concentration pathway 8.5 model (Fig. 9) is not greatly different from the representative concentration pathway 4.5 model (Fig. 8) but suggests greater suitability on parts of the Southern Tablelands and far less in the Northern Rivers hinterland.

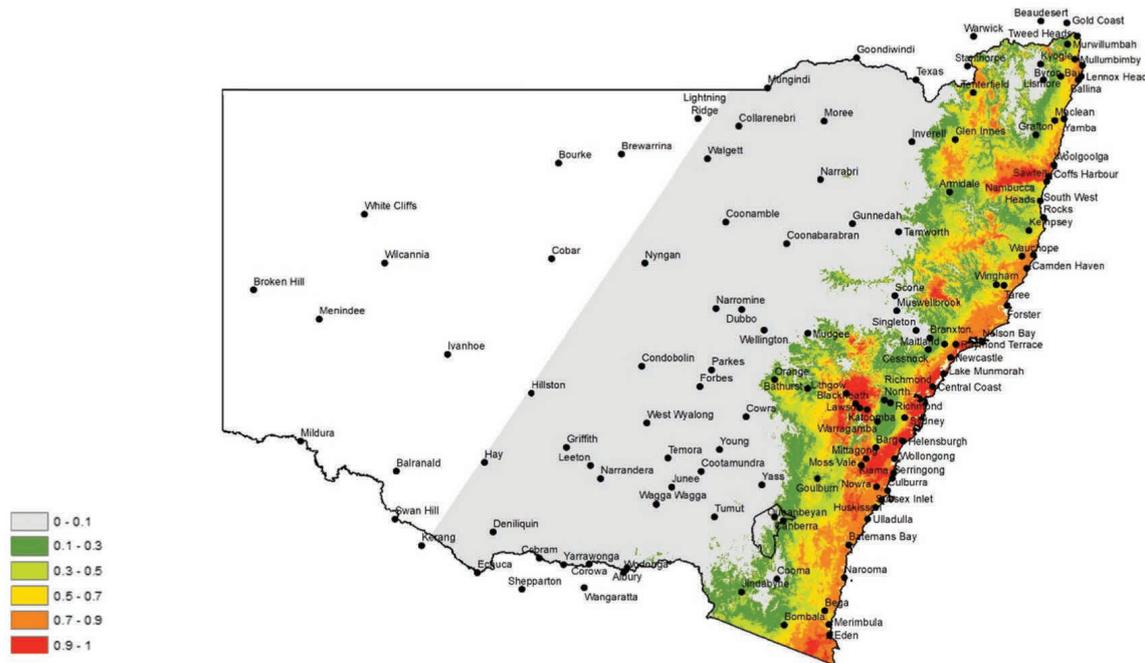


Fig. 8. Habitat suitability for *Phytophthora cinnamomi* under representative concentration pathway 4.5 (averaged over three climate models and ranked from 0 = unsuitable to 1 most suitable). The unshaded area was not assessed in the model as there were no presence or absence data there.

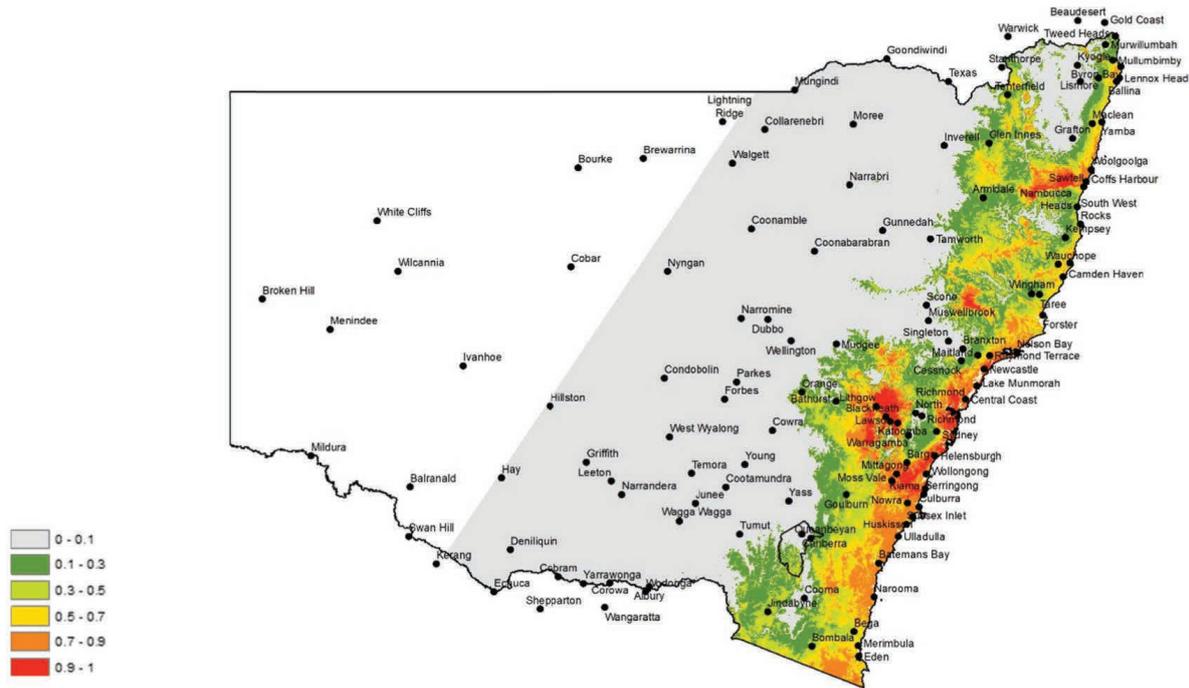


Fig. 9. Habitat suitability for *Phytophthora cinnamomi* under representative concentration pathway 8.5 (averaged over three climate models and ranked from 0 = unsuitable to 1 most suitable). The unshaded area was not assessed in the model as there were no presence or absence data there.

2) Susceptibility and distribution of assets at risk

Table 6 lists 258 NSW species from 47 families as being susceptible to infection by *Phytophthora cinnamomi*. The families with most susceptible species are Fabaceae (49 species), Myrtaceae (48), Proteaceae (31), Ericaceae (23),

Rutaceae (14) and Dilleniaceae (10). The genera with most susceptible species are *Eucalyptus* (33 species), *Pultenaea* (16), *Acacia* (13), *Hibbertia* (10), *Grevillea* (9), *Banksia* and *Prostanthera* (7). *Phytophthora cinnamomi* has been recovered from the roots of 14 threatened species.

Table 6. Susceptible species in NSW based on isolation of *Phytophthora cinnamomi* from wild, cultivated or glasshouse populations. Distribution is indicated by Botanical Regions (SC = South Coast, CC = Central Coast, NC = North Coast, ST = Southern Tablelands, CT = Central Tablelands, NT = Northern Tablelands, SWS = South West Slopes, CWS = Central West Slopes, NWS = North West Slopes, SWP = South West Plains, NWP = North West Plains, SFWP = Southern Far West Plains, NFWP = Northern Far West Plains). Threatened status in NSW (Biodiversity Conservation Act 2016) is indicated in parentheses after the species name (V = vulnerable, E = endangered, CE = critically endangered). The effect of *Phytophthora cinnamomi* will not necessarily be the same across the geographic range of a host species and many species will be asymptomatic under most environmental conditions.

FAMILY / Species	SC	CC	NC	ST	CT	NT	SWS	CWS	NWS	SWP	NWP	SFWP	NFWP	References
ANTHERICACEAE														
<i>Laxmannia orientalis</i>	✓													26, 27
APIACEAE														
<i>Actinotus helianthi</i>	✓	✓	✓	✓	✓	✓		✓			✓			5
<i>Xanthosia atkinsoniana</i>	✓	✓	✓	✓	✓	✓		✓						20
<i>Xanthosia dissecta</i>	✓	✓		✓	✓									4, 26, 27
<i>Xanthosia tridentata</i>	✓	✓	✓	✓	✓									5
ARAUCARIACEAE														
<i>Wollemia nobilis</i> (CE)					✓									3
ARECACEAE														
<i>Archontophoenix cunninghamiana</i>	✓	✓	✓											2
ASTERACEAE														
<i>Argentipallium obtusifolium</i>	✓													4, 27
<i>Cassinia aculeata</i>	✓	✓	✓	✓	✓		✓	✓		✓				15, 16, 21
<i>Coronidium oxylepis</i>	✓	✓	✓	✓	✓	✓		✓	✓		✓			21
<i>Ozothamnus obcordatus</i>	✓		✓	✓	✓	✓		✓	✓		✓			21

FAMILY / Species	SC	CC	NC	ST	CT	NT	SWS	CWS	NWS	SWP	NWP	SFWP	NFWP	References
ATHEROSPERMATACEAE														
<i>Atherosperma moschatum</i>				✓	✓	✓								15
BLECHNACEAE														
<i>Blechnum wattsi</i>	✓	✓	✓	✓	✓	✓								15
CASUARINACEAE														
<i>Allocasuarina paludosa</i>	✓	✓		✓	✓									4
<i>Allocasuarina rigida</i>			✓			✓			✓					21
<i>Allocasuarina torulosa</i>	✓	✓	✓		✓	✓		✓	✓					16
<i>Allocasuarina verticillata</i>	✓	✓		✓	✓		✓	✓	✓	✓				14, 16
<i>Casuarina cunninghamiana</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			16
<i>Casuarina obesa</i>										✓		✓		6
COLCHICACEAE														
<i>Burchardia umbellata</i>	✓	✓	✓	✓	✓		✓	✓						28
CUNONIACEAE														
<i>Bauera rubioides</i>	✓	✓	✓	✓	✓	✓								14, 15, 19, 26
<i>Eucryphia moorei</i>	✓	✓		✓	✓									21
CUPRESSACEAE														
<i>Callitris rhomboidea</i>	✓	✓	✓		✓	✓								27
CYPERACEAE														
<i>Gahnia grandis</i>					✓									15
<i>Gymnoschoenus sphaerocephalus</i>	✓	✓	✓	✓	✓	✓								15
<i>Lepidosperma laterale</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			16
DENNSTAEDTIACEAE														
<i>Pteridium esculentum</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			16
DILLENIAEAE														
<i>Hibbertia acicularis</i>	✓	✓	✓	✓	✓	✓		✓	✓					15, 19
<i>Hibbertia calycina</i>				✓	✓									1
<i>Hibbertia circinata (CE)</i>	✓													25
<i>Hibbertia cistiflora</i>		✓			✓	✓								26
<i>Hibbertia empetrifolia</i>	✓	✓	✓	✓	✓									15, 19
<i>Hibbertia fasciculata</i>	✓	✓	✓	✓	✓									27
<i>Hibbertia obtusifolia</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		21
<i>Hibbertia procumbens (E)</i>		✓												15, 19
<i>Hibbertia riparia</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		15, 19, 26
<i>Hibbertia virgata</i>	✓	✓								✓		✓		26
ERICACEAE														
<i>Acrothamnus maccraei</i>				✓										21
<i>Acrotriche serrulata</i>	✓			✓	✓	✓		✓						4, 15, 26, 27
<i>Astroloma humifusum</i>	✓	✓	✓	✓	✓		✓	✓	✓	✓				4, 15, 19
<i>Astroloma pinifolium</i>	✓	✓	✓	✓	✓									15, 19
<i>Brachyloma daphnoides</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓			26
<i>Epacris gunnii</i>		✓	✓	✓	✓									14, 15
<i>Epacris impressa</i>	✓			✓	✓									26
<i>Epacris obtusifolia</i>	✓	✓	✓	✓	✓	✓								15
<i>Epacris paludosa</i>	✓	✓		✓	✓									1
<i>Epacris petrophila</i>				✓										18
<i>Epacris purpurascens (V)</i>		✓		✓	✓									5
<i>Leucopogon ericoides</i>	✓	✓	✓	✓	✓			✓	✓					15, 19, 26
<i>Leucopogon esquamatus</i>	✓	✓	✓	✓	✓									1
<i>Leucopogon lanceolatus</i>	✓	✓	✓	✓	✓	✓			✓					16
<i>Leucopogon microphyllus</i> var. <i>pilibundus</i>	✓	✓		✓	✓	✓	✓	✓						21

FAMILY / Species	SC	CC	NC	ST	CT	NT	SWS	CWS	NWS	SWP	NWP	SFWP	NFWP	References
<i>Nematolepis squamea</i>	✓	✓	✓	✓	✓									14, 15, 16, 19
<i>Phebalium squamulosum</i> subsp. <i>alpinum</i>				✓										18
<i>Philotheca myoporoides</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓				21
<i>Philotheca virgata</i>	✓													15
<i>Zieria laevigata</i>	✓	✓			✓	✓					✓			21
SANTALACEAE														
<i>Exocarpos cupressiformis</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			21
SAPINDACEAE														
<i>Dodonaea boroniifolia</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			21
<i>Dodonaea viscosa</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	21
SELAGINELLACEAE														
<i>Selaginella uliginosa</i>	✓	✓	✓		✓	✓								4
STYLIDIACEAE														
<i>Stylidium graminifolium</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓					15, 19, 21
THYMELAEACEAE														
<i>Pimelea ligustrina</i>	✓	✓	✓	✓	✓	✓	✓							4
<i>Pimelea linifolia</i>	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓			26, 27
TREMADRACEAE														
<i>Tetratheca ciliata</i>	✓		✓	✓			✓							19, 26
<i>Tetratheca labillardierei</i>	✓			✓										15
<i>Tetratheca pilosa</i>	✓													15, 26
<i>Tetratheca subaphylla</i>	✓		✓	✓										12
WINTERACEAE														
<i>Tasmania lanceolata</i>	✓			✓	✓									14, 15, 19
<i>Tasmania purpurascens</i> (V)						✓								11
XANTHORRHOEACEAE														
<i>Xanthorrhoea australis</i>	✓			✓										12, 26
<i>Xanthorrhoea glauca</i> subsp. <i>glauca</i>			✓			✓			✓					12
<i>Xanthorrhoea resinosa</i>	✓	✓			✓									12, 26
ZAMIACEAE														
<i>Macrozamia communis</i>	✓	✓	✓											4, 12, 16

References: 1. Barker & Wardlaw (1995); 2. Brown (1998); 3. Bullock et al. (2000); 4. David Cahill (Deakin University) pers. comm., extracted from: O'Gara et al. (2006); 5. Fraser (1956); 6. Gardner & Rokich (1987); 7. Gerretson-Cornell (1986); 8. Lee & Wicks (1977); 9. McCredie et al. (1985) - only plants dying after inoculation are listed; 10. McDougall & Liew, unpublished data; 11. McDougall & Summerell (2003a); 12. McDougall & Summerell (2003b); 13. Podger & Batini (1971); 14. Podger & Brown (1989); 15. Podger et al. (1990b); 16. Pratt & Heather (1973); 17. Reiter et al. (2004); 18. Rigg et al. (2018); 19. Schahinger et al. (2003); 20. Shearer & Dillon (1996); 21. Taylor (1974); 22. University of Pretoria (2002); 23. Vickery (1997); 24. Wan et al. (2019); 25. Wan, McDougall & Liew (unpublished data); 26. Weste (2001); 27. Weste et al. (2002); 28. Wills (1993).

Species known to be susceptible to *Phytophthora cinnamomi* with a strong gradient from east (high suitability) to west have a modelled distribution similar to the pathogen itself (low suitability) (Fig. 10).

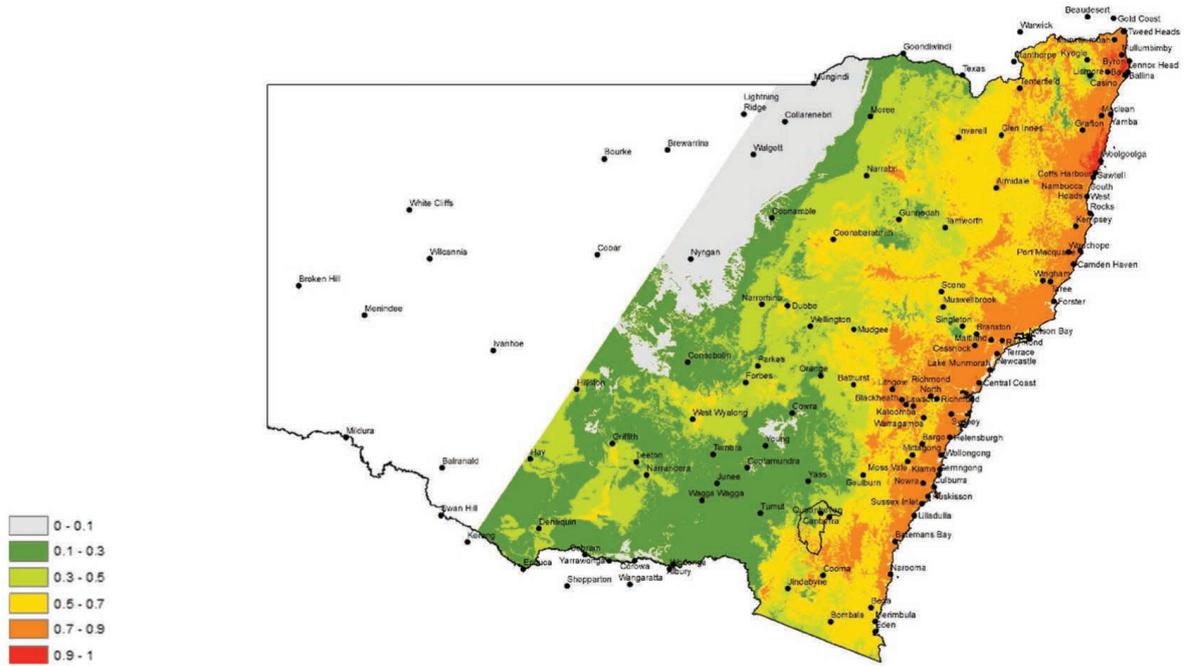


Fig. 10. Species distribution model of assets (threatened species), ranked from 0 = unsuitable to 1 most suitable.

3) Risk

Current and future risk mimics *Phytophthora cinnamomi* habitat suitability; i.e. the more suitable the habitat the more threatened species tend to be present, and the higher the risk (Figs. 11 - 13). Of the 585 listed threatened flora (<https://www.environment.nsw.gov.au/topics/animals-and-plants/threatened-species/saving-our-species-program>, accessed 19 Feb 2020) occurring within the modelled area, 402 species (69%) have at least one population in highly suitable habitat

for *Phytophthora cinnamomi* (raster cell value > 0.75). Two species known to be highly susceptible to infection by *Phytophthora cinnamomi* and occurring in single populations (*Hibbertia circinata* and *Prostanthera marifolia*) are probably at a high risk of imminent extinction because the pathogen is already present in the vicinity. The susceptibility of most threatened species is unknown but they may be considered at risk until the risk is adequately quantified.

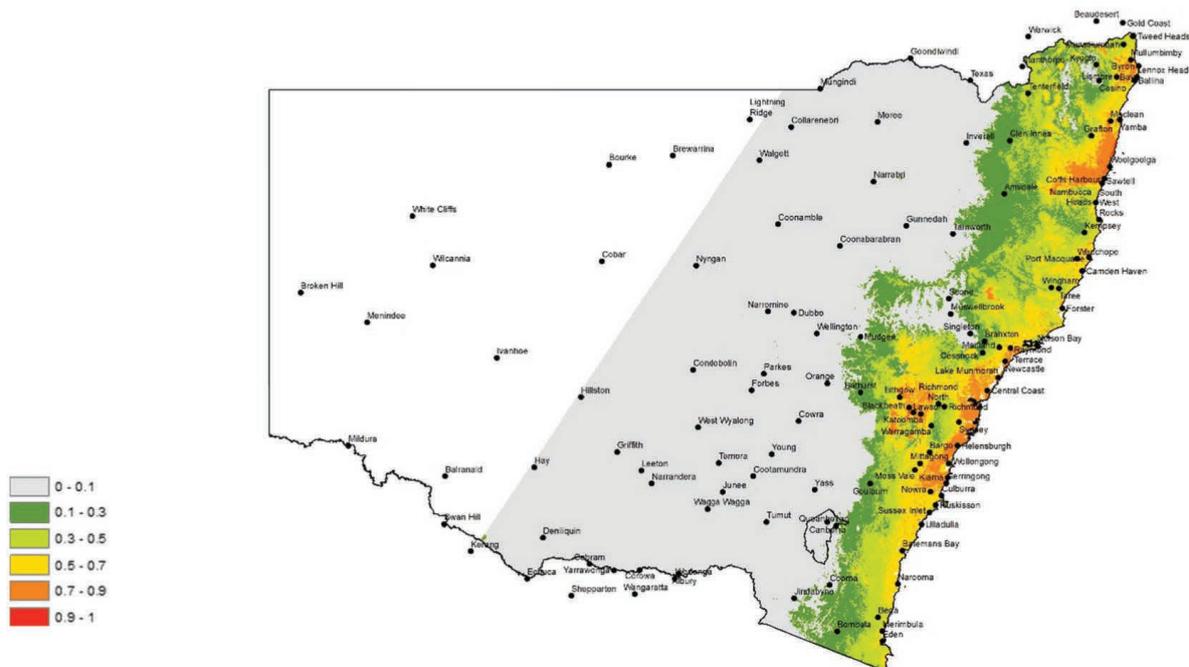


Fig. 11. Current risk to assets from the effects of *Phytophthora cinnamomi*. The map is the product of layers of habitat suitability for *Phytophthora cinnamomi* and assets (threatened species); 0 = no risk, 1 = highest risk.

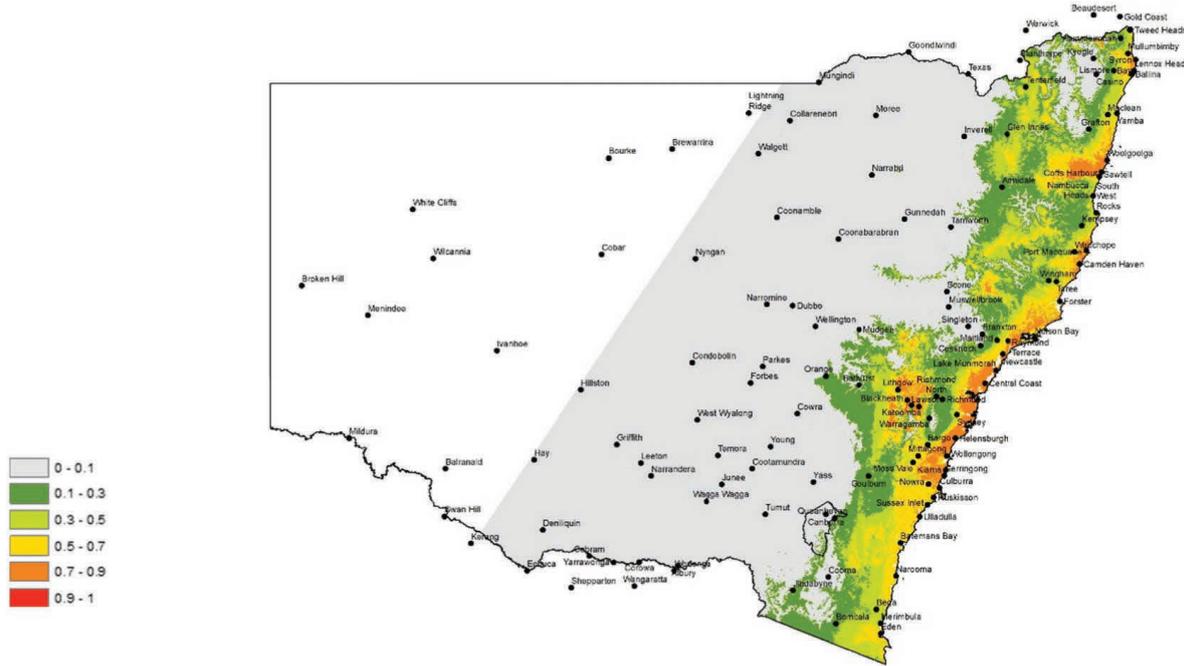


Fig. 12. Modelled risk to assets from the effects of *Phytophthora cinnamomi* in 2070 under representative concentration pathway 4.5. The map is the product of layers of habitat suitability for *Phytophthora cinnamomi* and assets (threatened species); 0 = no risk, 1 = highest risk.

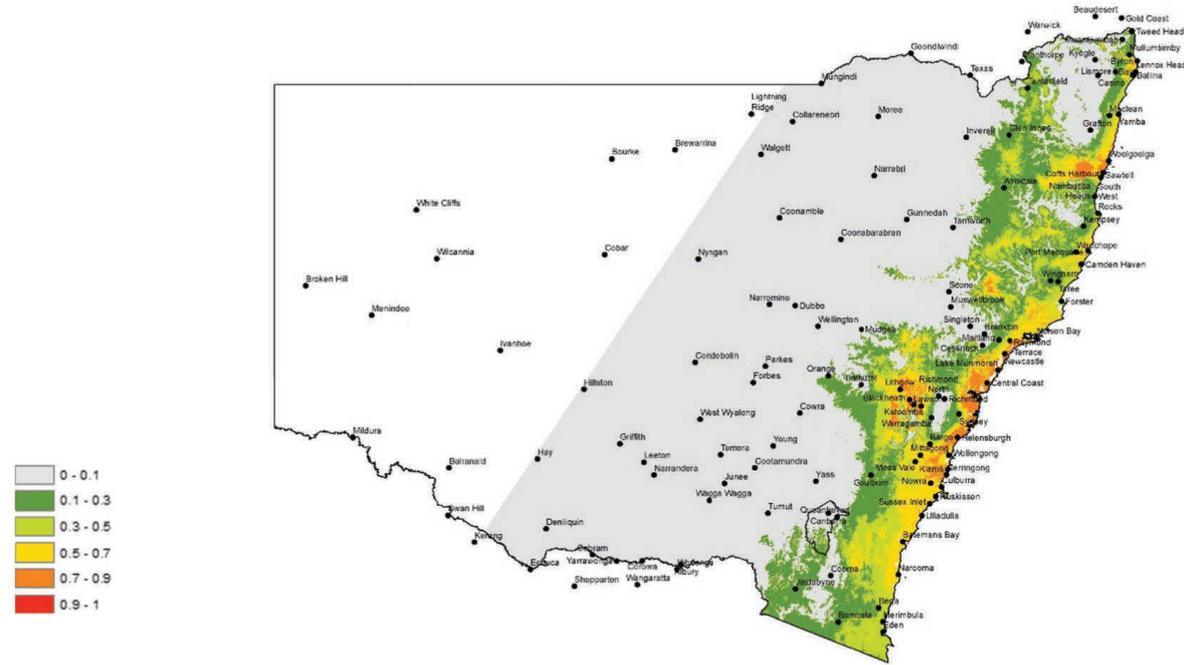


Fig. 13. Modelled risk to assets from the effects of *Phytophthora cinnamomi* in 2070 under representative concentration pathway 8.5. The map is the product of layers of habitat suitability for *Phytophthora cinnamomi* and assets (threatened species); 0 = no risk, 1 = highest risk.

Current and future risk tend to be greatest closer to the coast but the scale of the risk maps can hide local complexity. Mean risk, for instance, is currently very low in most IBRA regions of the study area but risk is locally high on the South Western Slopes, Brigalow Belt South and New England

Tablelands (Fig. 14a). The future risk across IBRA regions is not greatly different to current risk except that the mean risk in northern regions (especially South Eastern Queensland) is likely to decline whereas the maximum risk in the Australian Alps region is expected to increase (Fig. 14b).

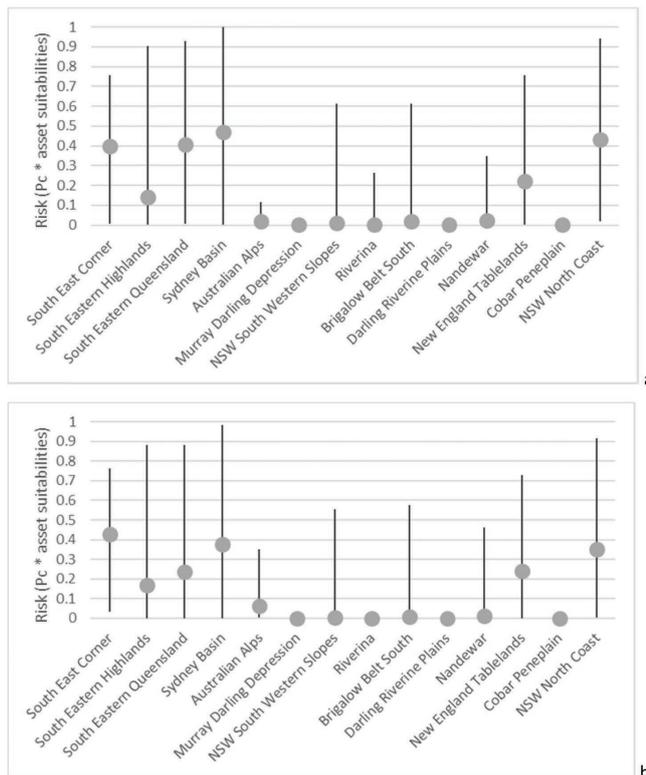


Fig. 14. Minimum to maximum risk for each IBRA region (line) and mean risk (grey dot), a) currently and b) in 2070 under representative concentration pathway 4.5.

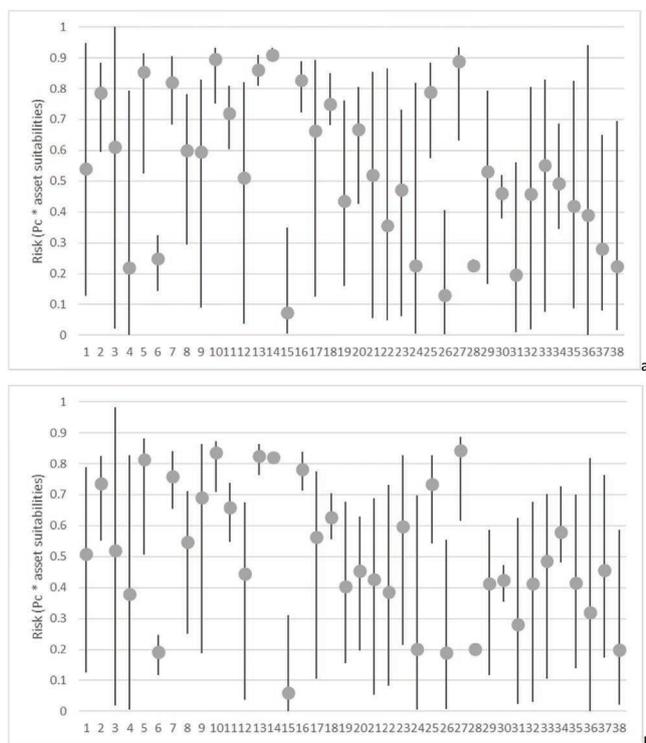


Fig. 15. Minimum to maximum risk for Protected Areas with 10 or more samples for *Phytophthora cinnamomi* (line) and mean risk (grey dot), a) currently and b) in 2070 under representative concentration pathway 4.5: 1. Barrington Tops NP, 2. Berowra Valley NP, 3. Blue Mountains NP, 4. Border Ranges NP, 5. Brisbane Water NP, 6. **Bungonia NP**, 7. *Dharawal NP*, 8. **Dharug NP**, 9. Dorrigo NP, 10. *Garigal NP*, 11. *Georges River NP*,

12. *Gibraltar Range NP*, 13. *Heathcote NP*, 14. **Kamay Botany Bay NP**, 15. **Kosciuszko NP**, 16. *Lane Cove NP*, 17. **Morton NP**, 18. *Mount Hyland NP*, 19. Mummel Gulf NP, 20. **Nadgee NR**, 21. **Nattai NP**, 22. New England NP, 23. Nightcap NP, 24. Oxley Wild Rivers NP, 25. *Popran NP*, 26. **Richmond Range NP**, 27. *Royal NP*, 28. *Scheyville NP*, 29. South East Forest NP, 30. **Thirlmere Lakes NP**, 31. **Toonumbar NP**, 32. **Washpool NP**, 33. *Werrikimbe NP*, 34. Whian Whian SCA, 35. **Willi Willi NP**, 36. Wollemi NP, 37. **Wollumbin NP**, 38. Yengo NP (18). Reserves with a very low density of presence records (< 1 / 1000 ha) are shown in bold. Those with a high density of presence records (> 10 / 1000 ha) are shown in italics.

Similarly, many protected areas (National Parks, Nature Reserves etc.) have a wide range of risk now (Fig. 15a) and in the future (Fig. 15b). The response to the risk at this scale might be interpreted according to the number of presence records and size of the reserve. For instance, reserves with a very low density of presence records and high risk (e.g. Dharug NP, Kamay Botany Bay NP, Nadgee NR, Nattai NP, and Washpool NP) might focus management on containing existing infestations and using hygiene to prevent invasion of *Phytophthora cinnamomi* from external infested areas. Reserves with a very high density of presence records and high risk (e.g. Dharawal NP, Garigal NP, Georges River NP, Gibraltar Range NP, Heathcote NP, Lane Cove NP, Mount Hyland NP, Popran NP, Royal NP, and Werrikimbe NP) might focus more on asset protection.

Discussion

Phytophthora cinnamomi distribution

The distribution of *Phytophthora cinnamomi* has been modelled in other areas (e.g. locally - Royal National Park, Keith et al. 2012; regionally - southwest USA, Thompson et al. 2014; globally, Burgess et al. 2017a). However, models can be difficult to compare because they use different sets of explanatory variables, different analytical approaches and are of different scales. Despite that, Duque-Lazo et al. (2016) concluded that *Phytophthora cinnamomi* distribution was driven by different variables in WA and Spain, when using uniform methodologies and variables. This probably reflects the broad environmental niche of this pathogen and its diverse host range. In NSW, it has been found in areas with both high summer rainfall (northern coastal areas) and low summer rainfall (southern tablelands areas), and with both low winter temperatures (tableland areas) and moderate winter temperatures (coastal areas). There does, however, appear to be consistency in the lower limit of mean annual temperature in relation to habitat suitability and impact. Podger et al. (1990a) modelled *Phytophthora cinnamomi* in Tasmania and hypothesized that damage caused by it is unlikely to occur in native vegetation below the 7.5°C isotherm. In the current study there were no records of *Phytophthora cinnamomi* in areas with a mean annual temperature below 9°C. The most important variables in the distribution model when included were Bio5 (mean maximum temperature of the warmest month), Bio7 (temperature annual range = mean maximum minus mean minimum temperature) and Bio12 (annual precipitation). Summer temperature was found by

Duque-Lazo et al. (2016) to be important in the distribution of *Phytophthora cinnamomi* in Andalusia, Spain (mean temperature) and Western Australia (maximum temperature). Summer and the warmest month will often be times of water stress for plants, and when they are most vulnerable to infection by pathogens.

Phytophthora cinnamomi is widespread in eastern NSW and rare west of the Great Dividing Range. It appears to be very rare on the Riverine plains to the west and absent in the Australian Alps bioregion, reflecting the climatic constraints of temperature and rainfall for *Phytophthora cinnamomi* presence; i.e. modelled mean maximum temperature in the warmest month mostly between 22.1 and 30.6°C, and modelled annual precipitation mostly between 619 and 1871 mm. Low modelled habitat suitability in the Hunter Valley may be partly because there has been little sampling there but additional sampling done in the current study also failed to detect *Phytophthora cinnamomi*.

Within the area of optimum habitat suitability on the eastern edge of NSW, *Phytophthora cinnamomi* is often found on sandstone substrates, perhaps favoured by perched water tables and impeded drainage above rock shelves (Fig. 16). It is also found commonly on cleared land reflecting the importance of disturbance in dispersal. Several forest and heathland types of the Sydney and South Coast area have more records of *Phytophthora cinnamomi* than expected, while in northern NSW, warm temperate rainforest is especially invaded. However, high suitability does not always reflect impact and so plants in rainforests typically show few or no symptoms when the pathogen is present (McDougall & Summerell 2003b).



Fig. 16. Heathy forest on edge of Bamarang National Park. Water commonly pools above the sandstone shelf. *Phytophthora cinnamomi* was detected in the skeletal soil at this site though few plants were apparently in poor health.

Climate projection models to 2070 under two emission scenarios predict a decline in habitat suitability in northern NSW and an intensification of suitability in southern NSW (including the Southern and Central Tablelands). This does not mean that *Phytophthora cinnamomi* will be of no concern in far northern NSW in the future but its effects might be seen

less often. An increase in habitat suitability in the Australian Alps will mean that new highly susceptible hosts are likely to come into contact with this pathogen (Rigg et al. 2018). Hygiene will be difficult to enforce in the Alps because of high visitation but is worth pursuing in remote areas.

In the species distribution model for *Phytophthora cinnamomi*, 94% of presence records had a habitat suitability of > 0.5, which suggests that the model performed well in predicting where the pathogen is now. However, 69% of absence records also had a habitat suitability > 0.5. The most likely explanation for this apparent anomaly is that, for many sites where *Phytophthora cinnamomi* was not detected in soil samples, the pathogen either had not yet arrived at the site or it was not detected in the sample taken. In some cases though, the explanation may lie in local site characters being antagonistic to pathogen presence. *Phytophthora cinnamomi* is known to have poor survival and minimal impact in some soil types (e.g. highly organic soils (Halsall 1982), those with high levels of nitrogen or calcium (Broadbent and Baker 1974, Trochoulis et al. 1986)), perhaps relating to soil microbial composition (Halsall 1982). Under some circumstances, nitrogen may also exacerbate symptoms, although this is apparently species-specific (Scarlett et al. 2013). The interactions between host, pathogen activity, soil nutrition and microbes are clearly complex. On the Perth coastal plain of Western Australia *Phytophthora cinnamomi* has a large impact on vegetation in one dune type but not on another with similar vegetation (Shearer & Dillon 1996). During field surveys for the current study we noticed that susceptible species were often unaffected in near coastal vegetation with deep sandy soils, and *Phytophthora cinnamomi* was rarely recorded, despite heavy disturbance from vehicles and intense coastal development (Fig. 17). Within areas identified from modelling as being highly suitable for this pathogen, not all are apparently threatened to the same extent, at least not under current conditions. The reasons for some areas being unfavourable to *Phytophthora cinnamomi* despite favourable climate, the presence of susceptible species and local disturbance is worth further investigation. These areas may become refuges for threatened species at risk from *Phytophthora cinnamomi*.



Fig. 17. This forest near Seal Rocks (North Coast) contained species likely to be susceptible to *Phytophthora cinnamomi*

(e.g. *Xanthorrhoea* spp., *Banksia* spp.) but the pathogen was not detected in several samples, and no symptomatic vegetation was observed yet the site is below a popular tourist road and has a management trail through it. The absence of *Phytophthora cinnamomi* is surprising considering local disturbance and an abundance of dispersal vectors.

Susceptible species distribution and risk

More than 250 native NSW plant species are known to be susceptible to infection by *Phytophthora cinnamomi*. The real number is likely to be much greater because few have been tested for susceptibility. However, susceptibility to infection is not always a good indication of impact and risk. The genus *Eucalyptus* for instance may have the most known susceptible species in NSW but they are rarely killed by the pathogen. Many *Pultenaea* species, on the other hand, are killed when infected. Much of the information about the susceptibility of *Eucalyptus* species came from testing following concerns about the effect of *Phytophthora cinnamomi* on production forestry (e.g. Podger & Batini 1971) whereas few other species have been tested because they are not of commercial interest. That does not mean that eucalypts cannot be affected by *Phytophthora cinnamomi*. Indeed, some are affected as seedlings. *Eucalyptus sieberi* cotyledons, for instance, have been used as baits for *Phytophthora cinnamomi* because they are very sensitive to infection (McDougall et al. 2002). *Phytophthora cinnamomi* may also contribute to poor health in eucalypts when they are stressed by other factors (e.g. drought, flooding or insect attack) and this may be exacerbated by climate change. The mortality of susceptible species in the other genera listed above is variable, although deaths of *Acacia* species associated with *Phytophthora cinnamomi* infection are unknown in NSW.

Assets (i.e. threatened plant species) at potential risk from *Phytophthora cinnamomi* have a similar distribution to the pathogen itself, with a higher concentration of species predicted to occur closer to the coast. Because the habitat suitability and asset maps are so similar it is not surprising that the risk map is also similar, with highest risk close to the coast. Despite that broad pattern, risk will often be locally high where new disturbances are introduced to uninfested native vegetation in areas with a high likelihood of pathogen occurrence; i.e. eastern NSW, and coincidentally where the greatest disturbance pressure occurs. Consideration of risk will be especially important in peri-urban areas, where housing development is encroaching on native vegetation. It will also be important where new recreational infrastructure and corridors (e.g. camping grounds, roads, walking tracks, horse-riding trails) are being placed in protected areas.

As was clear from interrogating the risk map by IBRA regions and national park (Figs. 14 and 15), the small scale of the risk map in Fig. 11 belies the variability at a larger scale. It is important, however, not to interrogate the maps too closely. Model resolution is 1 km² but the layers from which the models were built came from downscaled data collected from sparse weather stations. The species distribution models have little reliability at a fine scale. We recommend the maps

are used for their broad patterns of risk and interrogated for local variability within management units – e.g. an area has uniformly high risk or highly variable risk etc.

Management of *Phytophthora cinnamomi* in NSW

Little can be done once *Phytophthora cinnamomi* becomes established at a site. Eradication is costly and impractical in most situations (Dunstan et al. 2010). The primary aim of management always should be to keep the pathogen out of sites that are uninfested. Hygiene measures such as boot cleaning and vehicle washdown may be used but, to eliminate risk, these rely on universal uptake, which is difficult to achieve (Massenbauer 2018). Their careful design can, however, greatly reduce risk. The risk of spread is greatest when soils are wet, so temporary track and road closures may be effective after heavy rain in areas with susceptible species and vegetation. Managing drainage so that infected water does not flow into uninfested sites is also important. Application of fungistatic chemicals and ex-situ conservation are last resorts. The primary fungistatic chemical available for control of *Phytophthora cinnamomi*, phosphite (active ingredient HPO₃⁻), can be applied as a spray or by injection (e.g. see Komorek and Shearer 1997). Dose concentration and frequency differ between species and need to be determined empirically. Phosphite can be phytotoxic (e.g. Pilbeam et al. 2000) and there is some evidence of the development of resistance to its application (Hunter 2018). When effective, phosphite gives susceptible plants resistance to the effects of infection (McComb et al. 2008); it does not kill the pathogen. Phosphite is currently not licensed for broadscale use in native vegetation in NSW.

In WA and parts of the southern States, the presence of *Phytophthora cinnamomi* can often be assessed with some certainty if symptomatic susceptible species are present (Department of Conservation and Land Management 2001). Interpretation of diseased sites does become more difficult with time since infestation but interpretation can often be done without soil sampling. This is not the case in most of NSW where symptoms are rarely obvious or confidently attributed to *Phytophthora cinnamomi*. Remote sensing may assist in identifying areas affected by pathogens in the future (Newby et al. 2019) but for now, confirmation of an infestation of *Phytophthora cinnamomi* typically requires soil sampling.

Even when symptoms are apparently obvious, *Phytophthora cinnamomi* may not be the cause. We sampled three areas of extensive dying *Xanthorrhoea glauca* subsp. *glauca* on the Southern Tablelands. All populations displayed leaf yellowing and stem collapse (Fig. 18), symptoms commonly seen in affected populations of other *Xanthorrhoea* species in Australia (and even *Xanthorrhoea glauca* subsp. *angustifolia* in northern NSW (McDougall and Summerell 2003b)). *Phytophthora cinnamomi* was not found in numerous soil samples. The failure to detect the pathogen at these sites means only that the pathogen was not detected, not that it was absent. Additionally, most of the new presence records from the current study came from areas with asymptomatic

vegetation. So, in NSW, *Phytophthora cinnamomi* is already widespread and often present without causing apparent effects on resident plant species, apparent effects on resident plant species are not always attributable to the pathogen, and soil sampling will not always detect the pathogen. How is something like this managed? Here we attempt to provide guidance to those tasked with managing this perplexing but destructive organism in NSW.



Fig. 18. A population of *Xanthorrhoea glauca* near Lake George (Southern Tablelands). Plants of all sizes were dying but *Phytophthora cinnamomi* was not detected in numerous soil samples.

A case study of Phytophthora cinnamomi detection, impact and management (Mount Imlay)

Mount Imlay is an isolated peak (888 m above sea level) on the far south coast of NSW. The tenure is national park. It is surrounded by hardwood production forests and has long been the destination of a popular walk. A rough vehicle track once reached the summit from the south but is now closed. A communications tower was placed on the summit in the late 1990s. The peak is home to three endemic plant species, two of which are listed as threatened. The lower slopes of the mountain are forest dominated by *Eucalyptus sieberi* (Silvertop Ash). Below the rocky summit there is a ring of forest dominated by *Eucalyptus fraxinoides* (White Ash) while the summit area contains diverse heath with scattered, stunted *Eucalyptus sieberi*. The area was severely burnt in January 2020.

Phytophthora cinnamomi was first detected in soil samples from the summit in 1999 before the communications tower was erected and in response to poor health in plants of one of the threatened species (*Eucalyptus imlayensis*). Surveys of plant health in the following years detected the pathogen in the roots of five symptomatic species (McDougall and Summerell 2003b). Roots were sampled instead of soil to be more confident that *Phytophthora cinnamomi* was the cause of the symptoms. The most abundant species affected (*Xanthorrhoea australis*) has since disappeared from a large area of the northern ridge of the mountain and the diverse understorey replaced by tolerant grasses and *Lomandra confertifolia*. The trunks of *Xanthorrhoea australis* decompose within two years of death (Duncan and Keane

1996) and so there is now little evidence of the understorey diversity once common there.

Managing *Phytophthora cinnamomi* on Mt Imlay has involved addressing five questions:

- 1) Where is the pathogen?
- 2) What is at risk?
- 3) How is the pathogen dispersed?
- 4) Can dispersal be managed?
- 5) What else can be done?

The first question was addressed with soil sampling along the main walking track to the summit. *Phytophthora cinnamomi* was found in few samples but, based on the location of root samples that had tested positive, it was clear that it was present along the entire track apart from two sections in healthy *Xanthorrhoea australis*. Testing was not done in more remote sections of the park. The pathogen is assumed to be widespread because it was found on the summit and would have been dispersed downhill to much of the park by runoff.

Unlike most parts of NSW, the vegetation of Mount Imlay appears to be a good indicator of *Phytophthora cinnamomi* absence (i.e. where *Xanthorrhoea australis* is present and healthy) and presence (i.e. where *Xanthorrhoea australis* is absent and the understorey has few shrubs and forbs). So, the second question was simple to answer. Diverse healthy understorey vegetation was at risk. The glasshouse susceptibility of two of the three endemic plant species has since been tested. One (*Eucalyptus imlayensis*) does not appear to be susceptible. The other (*Hibbertia circinata*) is highly susceptible (Wan et al. unpublished data).

Phytophthora cinnamomi probably arrived on the mountain on vehicles or on the boots of bushwalkers. While runoff and gravity may have dispersed it from there to remote parts of the park, the main assets at risk are situated on the walking track, which follows a ridge from the north. Relocating the walking track is not possible because of the terrain. Closing the walking track is impractical because the walk is iconic and the country is very open – preventing access would be impossible. So, currently, bushwalkers are the main dispersal threat but they are not easily managed.

Boot scrubbing stations have been established at both ends of the main uninfested area with information about the disease threat for bushwalkers. Boot scrubbing may be effective because the local soil does not readily adhere to boots but it takes only one carrier to introduce the pathogen and cause disease. Aerial spraying with phosphite may be possible because the disease-free area is not large. This has been used for control of *Phytophthora cinnamomi* in Western Australia, although it may not be as effective as stem injection or on-ground spraying (Crane & Shearer 2014). Material for propagation of rare and threatened species has been collected and will help create living collections at botanic gardens. Seed of these species will be collected and stored.

The prognosis for species affected by disease in Mount Imlay National Park is poor but its consequences are being managed. The questions addressed at Mount Imlay are the same as those required elsewhere for *Phytophthora* management in NSW. In many ways, managing *Phytophthora* is very similar to managing fire: i.e. determine where it is, how it will spread and where it will spread to, determine what it will affect if it isn't contained, and attempt containment (mindful of assets most at risk).

Conservation management scenarios for Phytophthora cinnamomi in NSW

1) *Phytophthora cinnamomi* is present

In NSW, the presence of *Phytophthora cinnamomi* in a conservation reserve is rarely catastrophic for species and vegetation. The pathogen is already widespread and many of its local effects may have happened decades ago. An appropriate response will involve determining:

- a) where the pathogen is by testing soil, especially in areas of poor plant health – if it proves to be very widespread, preventing its dispersal to areas beyond the reserve may be the only practical management response but if it is localised, containment by limiting dispersal to uninfested areas will be a worthwhile aim;
- b) what is at risk (e.g. susceptible species, especially those locally rare or threatened) – this will typically be poorly known but if no assets are at risk, again, preventing dispersal of the pathogen to areas beyond the reserve may be the only practical management response;
- c) how the pathogen may be dispersed (e.g. on roads, walking trails etc);
- d) whether dispersal can be managed - if the pathogen is for instance present on all roads, which are located on ridge tops, the chance of limiting spread will be low;
- e) whether anything else can be done (e.g. seedbanking).

2) Another *Phytophthora* species is present

Little is known about the effects of species other than *Phytophthora cinnamomi* on native vegetation in Australia. All are likely to be pathogenic but few are likely to have observable effects on native plant species. Most conservation reserves will contain *Phytophthora* species, and some of these species may be native and quite localised in their occurrence (e.g. Khaliq et al. 2019). The presence of a *Phytophthora* species is not cause for concern unless its presence is clearly linked to poor plant health. Although it can be difficult to confirm that link, regular monitoring of plant health is a vital component of vegetation management, and perhaps the only way disease associated with *Phytophthora* species will be detected. Apart from *Phytophthora cinnamomi*, species known to be associated with poor plant health in Australia include *Phytophthora cambivora* (Green 2016), *Phytophthora cryptogea* and *Phytophthora gregata* (especially in wetland vegetation; McDougall et al 2018), *Phytophthora multivora* (e.g. Scott 2011, Puno et al. 2015), and a range of recently described species in Western Australia

(see Belhaj et al. 2018). If any of these species is present in areas of symptomatic vegetation, an examination of its effects is warranted.

3) A reserve is in a high risk area but *Phytophthora cinnamomi* has not been recorded

In this case, *Phytophthora cinnamomi* may be absent or it may be present and not yet detected (or searched for). Soil testing to detect its presence will be worthwhile if there is vegetation in poor health, especially if susceptible species are present. If there is no reason to sample for *Phytophthora cinnamomi* presence, the reserve might be assumed to have no *Phytophthora cinnamomi*, and management directed at preventing spread along disturbance corridors (e.g. roads, power easements and walking tracks) from outside the reserve through hygiene measures. The presence of susceptible assets in a high-risk area should be identified and access to these species and communities minimised. Staff and contractors accessing areas with susceptible assets should practice preventative hygiene measures. General monitoring of plant health to detect *Phytophthora* impacts and planning for limiting its spread, if detected, are advisable.

4) A reserve is in a low risk area but has symptomatic vegetation

In most cases, poor vegetation health has a cause other than *Phytophthora cinnamomi* and, in recent years, drought has been an important cause of sick and dead plants. The symptoms of drought are very similar to those of plants affected by *Phytophthora cinnamomi*. Soil sampling from the root zone of symptomatic plants may confirm the presence of *Phytophthora cinnamomi*; unfortunately, it can't confirm its absence. Without a positive test, it is still reasonable to minimise soil movement from symptomatic areas to areas with similar healthy vegetation because other pathogens may be the cause.

Fire as a potential management tool

Fire is used to manage vegetation – might it also be used to manage *Phytophthora cinnamomi*?

Fire is unlikely to ever remove the pathogen. Soil temperature declines rapidly with depth during a fire (e.g. Bradstock & Auld 1995) and is probably lethal to *Phytophthora cinnamomi* only in the top one or a few cm depending on severity; *Phytophthora cinnamomi* has been recorded at depths of up to 5 m in *Banksia* woodland in WA (Shearer et al. 2010) where fire will never be influential. Fuel reduction methods had no effect on the incidence of *Phytophthora cinnamomi* detection in forest of North Carolina (Meadows et al. 2011). In some cases, fire frequency might be manipulated to promote the establishment of susceptible species while minimising the effect of *Phytophthora cinnamomi* (Regan et al. 2011).

Most of the evidence suggests that, on balance, fire is more likely to be beneficial to *Phytophthora cinnamomi* activity but its effects will be short-lived. A rise in water table following fire may make rhizospheres wetter and increase the risk to susceptible species but again this is typically short-lived

(e.g. Silberstein et al. 2013). In Western Australia, fire has been found to potentially increase the severity and extent of disease (Moore et al. 2014).

Under some circumstances, fire may be unfavourable to the pathogen but, again, the effect is short-lived. Marks et al. (1975) found a brief reduction in the *Phytophthora cinnamomi* population after experimental burns but the effect disappeared within a year. Fires may temporarily reduce the density of hosts where they are obligate seeders (e.g. some *Banksia* spp.) but root systems of resprouting hosts will persist after a fire and be available for infection. The abundance of resistant and even antagonistic species may increase after a fire (e.g. *Acacia pulchella* in WA, Shea et al. 1979), potentially reducing the activity of *Phytophthora cinnamomi*; however, the pathogen is known to survive in asymptomatic hosts (Phillips & Weste 1984; Crone et al. 2013) and so is unlikely to disappear where this happens.

Regardless of the direct association between fire and *Phytophthora*, soil disturbance activities associated with fire suppression are likely to be a major vector of spread. Reducing this risk in times of urgency is clearly challenging but is worth investigation – identifying the assets at most risk from these activities on fire planning maps will be a good start. Further research is required on the effects of fire on pathogen activity and host regeneration to determine if it may be used, as Regan et al. (2011) suggest, to manipulate disease expression. The recent severe fire on Mt Imlay, a place where there has been much sampling for *Phytophthora cinnamomi* in the past, may offer an opportunity to investigate such effects.

Conclusion

Phytophthora cinnamomi is widespread in eastern NSW. It occurs mostly in areas with annual rainfall > 600 mm and has not been detected by baiting in areas with mean annual temperature < 9°C. Climate change may shift habitat suitability southwards but the pathogen is not likely to be any less of a threat in NSW by 2070. The host range of *Phytophthora cinnamomi* in NSW is poorly known but most hosts are likely to be asymptomatic under normal conditions. Other stresses (e.g. drought, flooding and insect attack) may make species more susceptible to infection and death, and climate change will bring new hosts into contact with the pathogen. Some vascular plant species are highly susceptible to infection but in most cases the degree of threat is poorly known. In addition, plants may be susceptible but *Phytophthora cinnamomi* may not yet be present in wild populations or it may not be pathogenic under prevailing site conditions. Monitoring of the health of threatened susceptible species is critical.

Despite the prevalence of *Phytophthora cinnamomi* in eastern NSW, some areas remain unaffected even where there are vectors for its introduction and susceptible species present. The reasons for this require investigation. Such areas might become refuges for translocated susceptible threatened species. Alternatively, the site properties suppressing

Phytophthora cinnamomi activity might be reproduced *in vivo* to allow susceptible species to persist.

Prevention of spread through good hygiene is the primary tool in the land manager's armoury. Once introduced, eradication is impractical. The chemical phosphite may give protection to susceptible plants in infested areas but its use will often buy time rather than be a long term panacea. Seedbanking will be important insurance against the risk of extinction in the wild.

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Appendix 1. Reducing spatial bias in the data

We assessed two approaches for reducing spatial sampling bias according to: 1) distribution of positives (DP) - randomly reducing the density of positive samples across the

study area to no more than one / 10 x 10 km grid cell; 2) sampling effort (SE) – randomly reducing the density of samples in areas of dedicated surveys to match the density of all samples (positive and negative) elsewhere.

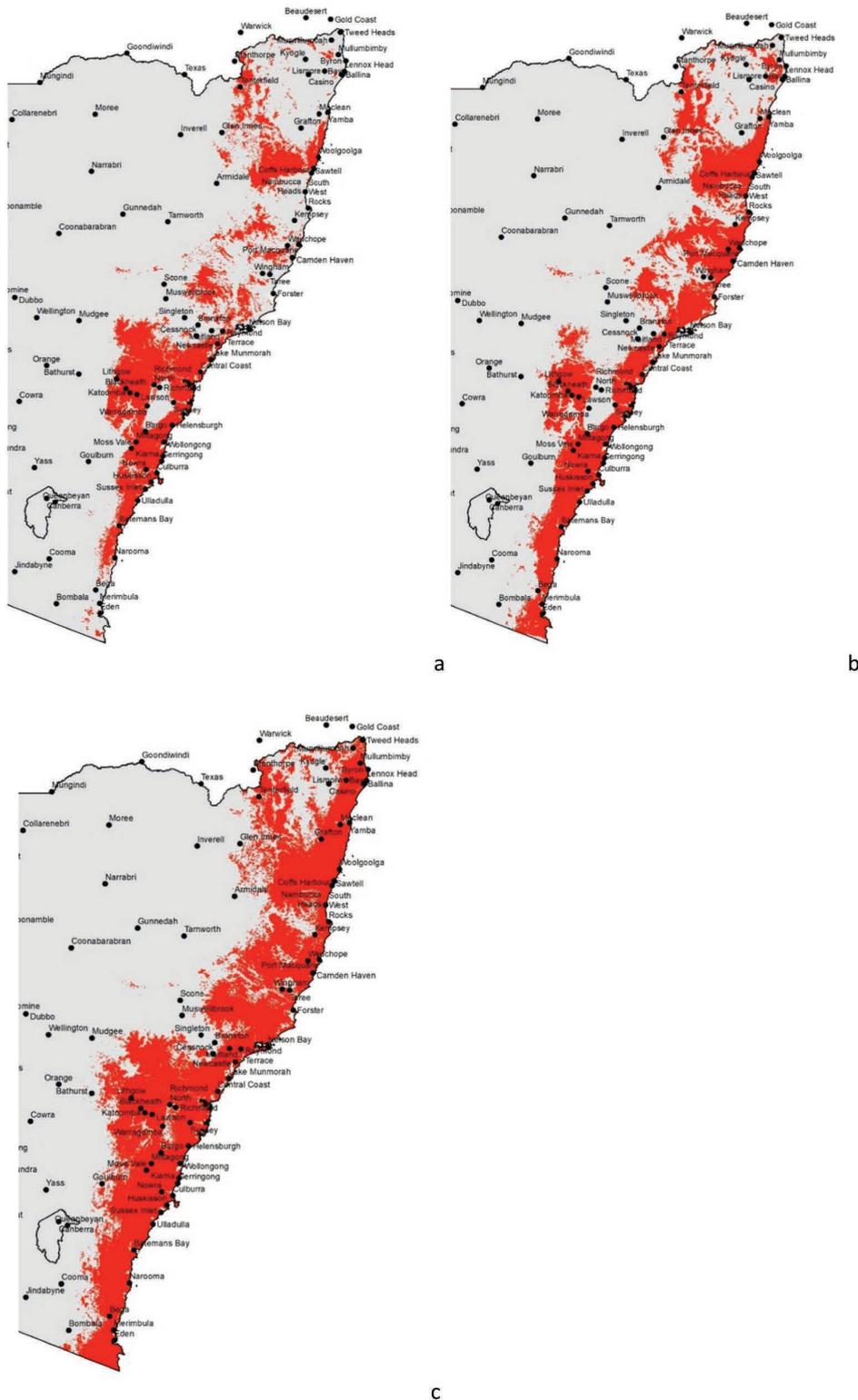


Fig. A1. Current habitat suitability for *Phytophthora cinnamomi* determined using a) using all available presence records (i.e. 1061 records); b) with bias reduction targeted at dedicated surveys (SE; 388 records); c) by randomly selecting one presence record in each 100 km² grid square (DP; 276 records). The red area indicates habitat suitability > 0.5 (i.e. greater suitability than areas shaded grey, < 0.5). Models were created using MaxEnt.

The model using raw data predicts the most suitable habitat for *Phytophthora cinnamomi* in the Blue Mountains and coastal plains around Sydney with minor areas of high suitability on the Barrington Tops and escarpment ranges above Coffs Harbour. Both of the bias reduced models predict highly suitable habitat along almost all the NSW coastline (Fig. A1) in addition to many of the areas identified by the raw model. On average, the DP model assigned higher suitability (mean = 0.81) to known presences than the other two models (mean = 0.73 and 0.75 for the raw and SE models respectively). In addition, omission (the assignment of low habitat suitability to samples where *Phytophthora cinnamomi* was present) was lowest for the DP model (Fig. A2). Accordingly, we reduced bias according to the DP data cleaning approach.

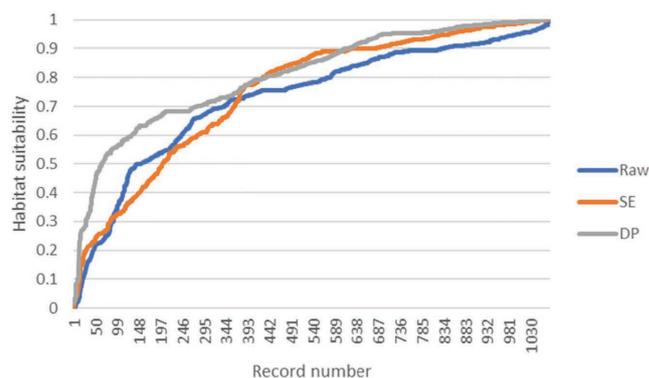


Fig. A2. Habitat suitability of presence records for *Phytophthora cinnamomi* in NSW with no data cleaning (Raw) and cleaning approaches based on sampling intensity (SE) and area (DP). Very few presence records using the DP cleaning approach were assigned very low habitat suitability (< 0.3); i.e. omission was low compared to the other approaches.

