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Title Page

Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens

Running Head: Climate change and *Phytophthora cinnamomi*

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Abstract

Globally, *Phytophthora cinnamomi* is listed as one of the 100 worst invasive alien species and active management is required to reduce impact and prevent spread in both horticulture and natural ecosystems. Conversely, there are regions thought to be suitable for the pathogen where no disease is observed. We developed a CLIMEX model for the global distribution of *P. cinnamomi* based on the pathogen's response to temperature and moisture and by incorporating extensive empirical evidence on the presence and absence of the pathogen. The CLIMEX model captured areas of climatic suitability where *P. cinnamomi* occurs that is congruent with all available records. The model was validated by the collection of soil samples from asymptomatic vegetation in areas projected to be suitable by the model for which there were few records. DNA was extracted and the presence or absence of *P. cinnamomi* determined by high throughput sequencing (HTS). While not detected using traditional isolation methods, HTS detected *P. cinnamomi* at higher elevations in eastern Australia and central Tasmania as projected by the CLIMEX model. Further support for the CLIMEX model was obtained by using the large dataset from southwest Australia where the proportion of positive records in an area is related to the Ecoclimatic Index value for the same area. We provide for the first time a comprehensive global map of the current *P. cinnamomi* distribution, an improved CLIMEX model of the distribution, and a projection to 2080 of the distribution with predicted climate change. This information provides the basis for more detailed regional scale modelling and supports risk assessment for governments to plan management of this important soil-borne plant pathogen.

Introduction

Worldwide, *Phytophthora cinnamomi* Rands is one of the most devastating plant pathogens, infecting a wide range of trees, woody shrubs and herbs (Cahill *et al.*, 2008; Weste & Marks, 1987; Zentmyer, 1980). The Global Invasive Species Database (<http://www.issg.org>) lists it as one of the 100 worst invasive alien species, and it is the only Oomycete, and one of only three plant pathogens listed (Lowe *et al.*, 2000). Although, the origin of *P. cinnamomi* remains uncertain, most evidence points to a natural distribution in mountainous regions in south-east Asia, *i.e.* in a temperate climate within the tropics (Arentz & Simpson, 1986; Jung *et al.*, 2016; Ko *et al.*, 1978; Martin & Coffey, 2012). *Phytophthora cinnamomi* was first described as the causal agent of stripe canker of cinnamon (*Cinnamomum burmannii*) in Sumatra (Rands, 1922). However, it is now known to have been the causal agent of ink disease of European chestnut, first reported in 1860 (Grente, 1961), and also of American chestnuts (*Castanea dentata*) prior to 1910 (Anagnostakis, 2001; Crandall *et al.*, 1945).

While *P. cinnamomi* can be a destructive pathogen globally in tropical and sub-tropical agriculture (Drenth & Guest, 2004), it is in ecosystems with a Mediterranean-type climate where it has its biggest impact. *Phytophthora cinnamomi* causes root rot and decline in the fynbos in the Cape Floristic Region of South Africa (Nagel *et al.*, 2013; Von Broembsen & Kruger, 1985). It is the dominant causal biotic agent in oak decline in Mediterranean Europe (Brasier *et al.*, 1993; Robin *et al.*, 1998; Vettraino *et al.*, 2002) and is also associated with oak disease in California (Garbelotto *et al.*, 2006). In the South-West Botanical Province of Western Australia (WA), an estimated 40% of the 5710 plant species, are susceptible to *P. cinnamomi*, including 14% considered highly susceptible (Shearer *et al.*, 2007). Given that *P. cinnamomi* is an Oomycete and free water is required for infection by zoospores, it is perhaps surprising that Mediterranean ecosystems are the most affected. However, the relatively

warm and wet winter and spring conditions are ideal for zoospore proliferation and host infection, while the long dry summers place plants, with compromised root or vascular systems, at risk of drought-induced mortality (Brasier, 1996; Desprez-Loustau *et al.*, 2006; Shearer & Tippett, 1989).

As *P. cinnamomi* has been transported globally with horticultural (perennial fruit, spice and nut crops), and has subsequently become invasive in many natural ecosystems, it would be very useful to predict parts of the globe where it might occur now and into the future. This would enable preventative measures to be implemented. Species distribution models (SDM) of invasive species can be poor if the organism is capable of invading new environments extending beyond the known niche of the species in its native range (Gallien *et al.*, 2010; Webber *et al.*, 2011). Additionally, as demonstrated for *Phytophthora ramorum*, an invasive species in North America and Europe, SDMs generated early in an invasion (2001) are less accurate than later models after the pathogen was closer to equilibrium (2009) (Václavík & Meentemeyer, 2012). However, the biology of *P. cinnamomi* is well known, and the species has a global distribution where it has been invasive for at least 100 years (Anonymous, 2015). Additionally, there are extensive distribution records available, especially across a wide range of climates in Australia where pathogen distribution has been well delineated, and is stable, representing an equilibrium situation. For these reasons, it is possible to develop a robust global species distribution model for *P. cinnamomi*.

Various modelling approaches have been used previously to estimate the potential distribution of *P. cinnamomi* in Europe (Brasier & Scott, 1994), France (Bergot *et al.*, 2004; Desprez-Loustau *et al.*, 2007), south-western Spain and south-western Australia (Duque-Lazo *et al.*, 2016) and south-western USA (Thompson *et al.*, 2014). Here we produce, for the first time, a global niche model for *P. cinnamomi* using a large empirical data set on the

presence and absence of *P. cinnamomi*. The objectives of this paper were to (1) model the global distribution of *P. cinnamomi*, (2) validate the distribution model in Australia by determining the presence of *P. cinnamomi* in 567 soil samples collected independently of symptoms of disease, and (3) model the global distribution of *P. cinnamomi* under the projected climate of 2080.

Materials and methods

Data sources

Global distribution data for *P. cinnamomi* was obtained from published literature (e.g. tables of locations and georeferenced distribution maps), national databases (e.g. Australia, Argentina, New Zealand) and personal communications (Table S1). Records were excluded if they could not be verified from primary literature sources. In total, 15, 234 presence and 20, 301 absence records were obtained from 11 countries. The majority (98%) of these were from Australia. Data were checked for plotting errors and converted to shape files.

CLIMEX parameters

We built a species distribution model using presence and absence data for *P. cinnamomi* using the semi-mechanistic modelling software CLIMEX (Michael *et al.*, 2012; Webber *et al.*, 2011; Yonow & Sutherst, 1998). CLIMEX models the response of a species to climate based on the organism's physiology, biology, seasonal phenology and geographical distribution (Kriticos *et al.*, 2015). The model is then projected globally using current climate (to test the model) and projected with a future climate scenario to estimate sensitivity to future climate changes. It is a method particularly suited to projecting presence and absence in novel current and future climates, allowing evaluation of risks associated with biological invasion and biosecurity (Sutherst & Bourne, 2009; Webber *et al.*, 2011).

CLIMEX contains a parameter set of five meteorological variables: average minimum monthly temperature (T_{min}), average maximum monthly temperature (T_{max}), average monthly precipitation (P_{total}) and relative humidity at 09:00 h (H09:00) and 15:00 h (H15:00). These are used to define weekly and annual indices that determine the species response to temperature and soil moisture. CLIMEX calculates an annual growth index based on the growth of an organism under favourable conditions of Temperature, Moisture and Light. Stress indices (cold, hot, wet and dry) and their interactions may also be added to the model to indicate species restriction during unfavourable conditions. The growth and stress indices are combined to create the Ecoclimatic Index (EI) (range from zero to 100), an estimate of the favourability of a particular location for the species.

The parameter values used in CLIMEX were initially determined from published sources (Table 1, S2). The distribution and annual phenology (i.e. the temperature and moisture indices were adjusted to reflect the weekly growth of the pathogen throughout the year) were used to guide an initial iteration of the temperature and moisture parameter values so that a justifiable fit between the model results and the biology and distribution was obtained. The next step was to add relevant stress parameters. Dry stress was fitted by starting with the CLIMEX model of Sutherst *et al.* (1999), which required little change to correspond to the positive records of the distribution across the dry gradient in WA. Hot stress was adopted from the CLIMEX model of Desprez-Loustau *et al.* (2007) and verified (and not changed) for inland Australia and for tropical regions.

Finally, two models were generated to take into account cold stress. Firstly, the records of presence and absence in eastern North America (Fig. 1B) were used as a guide in an iterative process to determine cold stress parameter values. This model produced values which did not corresponded to the observed distribution data for Tasmania (TAS). Consequently, a second

model was derived by changing the stress accumulation rate based on the historical records of presence and absence in TAS.

Model validation – High Throughput Sequencing in Australia

Presence/absence data for Australia are biased towards symptomatic vegetation because sampling is typically done to determine the cause of symptoms. Thus, if the pathogen survives in places where it does not cause symptoms, this could lead to an under-estimation of the *P. cinnamomi* distribution. We therefore collected 567 new samples from asymptomatic forest sites both within the current known climatic distribution of *P. cinnamomi* (eastern seaboard Australia from Victoria to north Queensland, TAS and WA) and beyond (e.g. high altitude areas of TAS, New South Wales and Victoria, and drier areas of WA). These samples were assessed by High Throughput Sequencing (HTS) to detect the presence of *P. cinnamomi* and consequently verification of the best CLIMEX model within Australia.

Additional soils were sampled during summer and autumn in 2013 and 2014 and 53 samples were collected from WA in spring 2015. At each sampling site between 8-12 sub-samples of rhizosphere soil (approx. 150 g) were taken at random within a 5 m radius at a depth of 2-15 cm. Each pooled soil sample (up to 2 kg) was air-dried, homogenized by sieving (2-mm mesh size), and a portion (60-80 g) was ground and homogenised using a TissueLyser LT (Qiagen). All samples were stored frozen at -20 °C after grinding.

DNA was extracted using the Mo Bio PowerSoil DNA isolation kit (MoBio Laboratories, Carlsbad, CA), according to the manufacturer's protocol, except for the first step where we replaced the buffer from the kit with 1 mL of saturated phosphate buffer (Na_2HPO_4 ; 0.12 M; pH 8) added to the soil sample (500 mg) according to a methodology proposed previously (Taberlet *et al.*, 2012) for extracellular DNA isolation. Genomic DNA from the soil samples

was amplified separately in duplicate. Amplicon libraries were performed using a nested PCR approach as described previously (Català *et al.*, 2015). The emulsion PCR reactions were carried out according to the Roche GS Junior emPCR Amplification Method Manual Lib-L (March 2012). The libraries were sequenced using Junior Genome Sequencer plates (454 Life Sciences/Roche Applied Biosystems, Nutley, NJ, USA). Bioinformatics was conducted in Geneious version R8 (<http://www.geneious.com/>).

Model validation – large dataset for south west Australia

The largest dataset of presence and absences covers the south west of WA (27, 068 records Table S1). This high density of records made it possible to relate the proportion of positive records to the value of EI as a test of the model. Only 10 x 10' cells with 10 or more records were included in the analysis. Cell location was determined by the fishnet (world grid polygon shapefile available from <http://www.climond.org/>), used in the CLIMEX output. The average (+ SE) number of records per cell included in the analysis was 120 + 11.6, (range 10 – 1097). ArcGIS was used to generate the data for the proportion of positive records and the EI value per cell.

Climate datasets

We used the CliMond gridded world climate dataset [Kriticos *et al.* (2012), see <http://www.climond.org/>], for both current climate (recent historical data centred on 1975) and future climate change scenario models. For the future climate scenario, the CSIRO-Mk3.0 global circulation model projected to 2080 was used; a period of time considered to allow sufficient change in climate to develop and the potential distribution of a short-lived and readily dispersed species such as *P. cinnamomi* to become apparent. The climate change scenario for 2080 is based on the IPCC emissions scenarios (the SRES scenarios or the Special Report on Emissions Scenarios) (Nakićenović & Swart, 2000). We used the A1B

scenario (IPCC 2007), which describes a future of very rapid economic growth, global populations that peak mid-century and decline thereafter and are balanced for future technological changes in fossil intensive and non-fossil energy sources. It provides a set of near mid-range values for global warming. The observed global carbon dioxide emissions during the 2000 – 2006 period are in line with, but above the IPCC's A1B emission scenario (Raupach *et al.*, 2007). The 2012 observations on emissions (Peters *et al.*, 2013) continue to be in line with this scenario. Because there is considerable uncertainty regarding future climate scenarios, this evaluation should be treated as an indicator of possible future *P. cinnamomi* range, rather than a comprehensive evaluation that accounts for uncertainty amongst ensembles of climate models.

Results

CLIMEX model based on historical climate

The historical climate suitability of *P. cinnamomi* was projected to the world to generate two models. The distribution of *P. cinnamomi* in North America (NA) was used to fix the cold stress for the NA model (Fig 1). Contributions of each parameter to the NA model are shown in Fig. S1, and the three stress values in Fig. S2. The NA model predicted suitability for *P. cinnamomi* including the central plateau in TAS (over 700 m) and the eastern Australian Alps (over 1200 m). These are regions for which there are no historical records for *P. cinnamomi* presence (Fig. 2). Consequently, a second model, the TAS model, was developed where the absence of *P. cinnamomi* above elevation of 700 m in TAS was used to set the cold stress (Fig. S3). The TAS model better reflected the known *P. cinnamomi* distribution in Australia, but did not match the records for North America.

In both models, regions of high suitability (EI>40) included most of western Europe, China, south-eastern Brazil and USA, New Zealand and much of coastal Australia. There were areas

of suitability in all countries or regions for which *P. cinnamomi* has been reported (Anonymous, 2015) (Fig. S4). The CLIMEX model also identifies many regions for which there are no occurrence records, but where climatic conditions are suitable for *P. cinnamomi*, most notably most of mainland China, Laos, Thailand, Burma and southern Sweden. Within Australia, absence for *P. cinnamomi* was recorded both outside the expected distribution (where it serves as a test of the model), but also within the distribution. Most positive detections were made within the modelled potential distribution. Exceptions were records from commercial orchards near Darwin in the Northern Territory and sites in the Riverina region of New South Wales and in Toowoomba, Queensland (Fig. 2).

Model validation – High Throughput Sequencing in Australia

Due to the discrepancy between the NA and TAS models based on historical distribution records, extensive sampling was conducted in regions of Australia projected to be suitable for *P. cinnamomi* by the NA model. This included the central plateau of TAS (>700 masl) and the Australian Alps (>1200 masl) (Fig. 3). Samples were also taken from drier regions of WA. Following analysis of HTS results, molecular operational taxonomic units corresponding to *P. cinnamomi* were detected in 245 of the 567 soil samples. When these new data points are included the distribution of *P. cinnamomi* now includes central TAS (Fig. 3), thus reflecting the NA model (Fig. 1). All other regions where *P. cinnamomi* was detected by HTS also fall within areas projected to be suitable by the NA model.

Model validation – large dataset for south west Australia

EI is determined in CLIMEX at a scale of 10 x 10' pixel. In WA, the region for which the most data were available, there are many positive and negative records within each pixel. Thus, it is possible to plot the ratio of positive records to the EI (Fig. 4). This produced a

significant positive relationship ($P < 0.05$), where higher EI was clearly associated with higher ratios of positive recoveries of *P. cinnamomi*.

Comparison to previous regional models

While not extrapolated to a global scale, there have been four previous CLIMEX models published for *P. cinnamomi* (Fig. S5). The main improvements in the new CLIMEX model (NA model) are found in the projection to tropical areas (where the pathogen naturally occurs in the uplands) and the northern hemisphere (better delineation of the northern limit due to cold stress). Three of the previous CLIMEX models projected that *P. cinnamomi* would persist across the tropics, to include all of Brazil, much of the Africa rainforest and all of south east Asia. In our new CLIMEX model these regions were excluded by lowering the temperature optimum and upper threshold. Regions in Australia known to be highly suitable for *P. cinnamomi* had low EI values in previous models. The model from Sutherst *et al.* (1999) was most similar to the new CLIMEX model, differing predominantly in the threshold for cold stress that was set in the current CLIMEX model based on *P. cinnamomi* distribution in North America.

A comparison of model sensitivity and prevalence were made for Australian and non-Australian data separately (Table 2). The proportion of Australia estimated to be climatically suitable for *P. cinnamomi* ranged from 0.10 for the Sutherst *et al.* 1999 model to 0.17 for one of the models of Desprez-Loustau *et al.* (2007) (Table 2A). Model sensitivity (i.e. percentage of records that fell within pixels predicted to be suitable by the model) ranged from 83% for the Sutherst *et al.* (1999) model to 98% for the NA model and 99% for the Desprez-Loustau *et al.* (2007) model. The comparison of model sensitivity for the world outside of Australia shows an improvement of the NA model (90%) over the TAS model and earlier versions including the model of Desprez-Loustau *et al.* (2007) (Table 2B). The prevalence ranged

from 10 to 24 with the NA model indicating 0.15 as the proportion of the world outside of Australia climatically suitable for *P. cinnamomi* persistence.

Potential Distribution under Climate Change

As global climates warm, potential distribution of *P. cinnamomi* will expand toward the poles, with regions formerly unfavourable due to cold stress now released from this constraint, most notably eastern and western Canada, eastern Europe, Iceland, Scandinavia and some parts of Patagonia (Fig 5, Fig. S6). While the landmass in the southern hemisphere is smaller, areas in southern Australia, New Zealand and Patagonia will become more suitable. Conversely many tropical, sub-tropical, and Mediterranean regions are projected to become less favourable, and contraction of suitable climate will be observed in much of southern China, central Africa, central America and South America (Fig 5).

Discussion

Horticulture and the transport of living plants was almost certainly the primary pathway for the introduction of *P. cinnamomi* into new regions (Zentmyer, 1985). However, its movement out of this managed environment into natural ecosystems is dependent upon climatic conditions suitable for the survival of the pathogen. The CLIMEX model presented here provides, for the first time, a comprehensive global distribution of *P. cinnamomi* incorporating world scale data collected from natural ecosystems. Where our model shows an EI of zero (i.e. unsuitable for persistence of *P. cinnamomi*), there is an absence of records of *P. cinnamomi* in natural environments. However, this does not exclude the possibility of *P. cinnamomi* existing in these regions, for example within avocado orchards, where the microclimate created by adequate water supply provides suitable conditions regardless of the general climate (Thompson *et al.*, 2014). The model is congruent with the hypothesis that the origin of *P. cinnamomi* is within the temperate uplands of Asia (Arentz & Simpson, 1986).

General details of the type locality and host for *P. cinnamomi* are given as “bark canker of cinnamon trees (*Cinnamomum burmanni*) in the uplands of the west coast of Sumatra”

(Rands, 1922). The CLIMEX model projection has a high EI value for the uplands of Sumatra. Most (85%) of the world’s cinnamon comes from Kerinci (Jambi Province) (Laumonier, 1997), also within the area of high modelled EI.

The only previous data available globally reported the presence of *P. cinnamomi* at a national or regional scales (Anonymous, 2015) and lacked the resolution provided here. There are several problems with these data. Firstly, a single detection is mapped as a whole country being considered as part of the distribution. Secondly, no host data are provided and many of the records are likely to be from managed environments not natural ecosystems. For example, although the map reports *P. cinnamomi* in Norway, extensive surveys within beech forests have not recovered *P. cinnamomi* in that country (Telfer *et al.*, 2015), suggesting the observation is unlikely to be from a natural system.

Our CLIMEX model is able to project suitability for *P. cinnamomi* in regions for which we could find no records, an important step forward in the understanding of the global distribution of this pathogen. Projections include most of mainland China, Korea, southern Sweden, Ethiopia, Laos, Thailand and Burma. *Phytophthora cinnamomi* has been detected in South Korean forests (Hyun & Choi, 2014), data missing from the CABI/EPPO map (Anonymous, 2015). While earlier surveys of oaks in southern Sweden have not recovered *P. cinnamomi* (Jönsson *et al.*, 2003), if introduced, our model predicts that *P. cinnamomi* could persist. For other regions, there are no records of *P. cinnamomi* occurrence from natural ecosystems, despite reports from orchards (horticulture). Additionally, *P. cinnamomi* was recently recovered from natural ecosystems in Vietnam (Table S1) and may be widespread in

natural environments in Asia without causing any obvious disease symptoms (Arentz & Simpson, 1986).

Our CLIMEX model fits very well with those presented previously at a regional scale; France (Marçais *et al.*, 2004, Marçais *et al.*, 1996), Europe (Brasier & Scott, 1994, Desprez-Loustau *et al.*, 2007), north-east USA (Balci *et al.*, 2007, McConnell & Balci, 2014). Recently, correlative SDM models were developed based on the presence or absence of *P. cinnamomi* from approximately 200 data points from southwest of Spain and 1, 000 data points from southwest WA (Duque-Lazo *et al.*, 2016). Models developed for Spain were not transferable to WA perhaps because of the vastly different landscapes that were compared, and the authors suggested caution with model transferability. Another correlative SDM was used to predict risk occurrence of *P. cinnamomi* in southwest USA taking into account climatic (winter temperature and spring rainfall) and edaphic factors such as soil carbon (Thompson *et al.*, 2014). This model is very detailed and accurate for the region in which it was produced but is unlikely to be transferable, especially to a global context.

Both the HTS records from across Australia and the large dataset from southwest WA provided robust tests for the model. Based on the HTS results, *P. cinnamoni* is more widespread than indicated by historical records in southern Australia, confirming the model based on *P. cinnamomi* distribution in North America .. The proportion of positive records in the large data set from southwest WA was positively correlated with the EI value. While obvious, this is the first time this approach, and the use of extensive sampling with a different methodology (classical plant pathology versus HTS) have been used for verification of species distribution models.

Hypotheses generated from modelling the distribution of P. cinnamomi

A core attribute of modelling distributions using CLIMEX is the identification of areas where a species has not been reported, but might be found (Kriticos *et al.*, 2015). Almost all point data available to us were congruent with the projected distribution; however there were areas for which no data were available. Thus, assuming that the origin of *P. cinnamomi* is south-east Asia, as supported by previous research (Arentz & Simpson, 1986; Jung *et al.*, 2016; Ko *et al.*, 1978; Martin & Coffey, 2012; Old *et al.*, 1984; Zentmyer, 1985), we propose three hypotheses to explain the absence of records; (a) *P. cinnamomi* is not present, (b) *P. cinnamomi* and disease expression is present, but due to lack of resources, interest or knowledge has not been reported, and (c) *P. cinnamomi* is present but due to various edaphic factors (e.g. pH) or lack of susceptible hosts, disease expression is not observed and hence there has been no need to look for a pathogen.

(a) *P. cinnamomi* is absent: Due to the ability of *P. cinnamomi* to be vectored by anthropogenic activities, it is likely that the pathogen is more widely distributed than has been mapped based on disease symptoms. Globally, both historically and contemporary movement is most likely in the plants-for-planting trade or associated with the transport of horticultural crops and woody ornamentals (Brasier, 2008; Callaghan & Guest, 2015; Eschen *et al.*, 2015; Scott *et al.*, 2013). Trade between Asia and the rest of the world has been ongoing for over 400 years, and *P. cinnamomi* is found globally in horticultural settings, providing *a priori* evidence to support its introduction to all regions where conditions are suitable for its survival. Once it has become established in a country or region, dispersal can occur by vehicles and heavy machinery carrying infested soil, poor nursery hygiene spreading the pathogen in container plants for out-planting, bushwalkers, and apiarists to name a few (Cahill *et al.*, 2008). In Australia, *P. cinnamomi* has been detected in almost all

regions projected by the CLIMEX model. Since it has been present in Australia from more than a century there is perhaps little potential for further spread under the current climate.

Globally, there are probably only a few climatically suitable areas with very low levels of disturbance that are free of the pathogen.

(b) Present, but not detected because of no infrastructure or experience: Many of the regions and countries indicated as suitable for *P. cinnamomi* in the CLIMEX model, but for which we could find no records, are less developed and may not have the resource infrastructure or reporting mechanisms to capture this information (Scott *et al.*, 2013). For example, all countries with over 20 known *Phytophthora* species are economically developed, with the United States, United Kingdom and Australia having the highest recorded species numbers (Scott *et al.*, 2013). Targeted sampling and public education in these regions could inform agencies of the potential threats of the disease, especially in new ventures and in biosecurity matters.

(c) Present, but not causing disease, so goes undetected: The CLIMEX model presented here maps the potential pathogen distribution, but not disease symptoms, and as such misses the nuances and subtleties that can shape pathogen impact on a regional scale. There are a number of possible reasons why plant communities/ecosystems may not be succumbing to *P. cinnamomi* despite its presence, including non-conducive climatic conditions (e.g. too cold, too dry for disease expression), edaphic factors such as disease-suppressive soils or high soil pH, or resistant plant species/communities (Broadbent & Baker, 1974; Malajczuk & McComb, 1979; Weste, 1974; Weste & Marks, 1987).

Under experimental conditions *P. cinnamomi* has a broad tolerance to pH (Benson, 1984; Byrt *et al.*, 1982), but survival and disease expression is very limited in alkaline soils (Alabouvette *et al.*, 1996; Broadbent & Baker, 1974). For example, *P. cinnamomi* is

completely absent from the narrow strip of calcareous soil on the Swan Coastal Plain in southwest WA, whereas it is widespread elsewhere in the same region [Shearer & Crane (2014)- this does not show on Fig. 2 because of the 10 x 10' scale]. Comparison of the CLIMEX model with data available for soil pH from the Atlas of the Biosphere (<http://nelson.wisc.edu/sage/data-and-models/atlas/index.php>). found that many of the regions climatically suitable for growth and development of *P. cinnamomi* have an alkaline soil pH, and as such the CLIMEX model probably overestimates suitability. Potentially unsuitable regions with high soil pH include the coast of North Africa, eastern Spain, parts of eastern Europe and Turkey, Uruguay and the Province of Buenos Aires in Argentina (Fig. S7).

Phytophthora cinnamomi is a poor saprotroph and competitor within the soil (McCarren *et al.*, 2005) and non-conducive soils, those rich soils with high soil carbon and high microbial activity, are suppressive to *P. cinnamomi* (Broadbent & Baker, 1974; Malajczuk & McComb, 1979; McDonald *et al.*, 2007; Nesbitt *et al.*, 1979; Weste & Marks, 1987). Many younger volcanic soils fit this category. This knowledge is utilised for disease management within avocado orchards, where mulch and lime are applied for *P. cinnamomi* control (Broadbent & Baker, 1974, Pegg & Giblin, 2008).

The presence and abundance of susceptible host species will determine where a pathogen is detected. In northern hemisphere forests a few tree species are susceptible such as oak (*Quercus* spp.) in Europe and North America, and pines (*Pinus* spp.) in eastern US. However, it is in the mega-diverse heathlands in Australia and South Africa where the greatest impact is observed, because so many of the species present are susceptible (Shearer *et al.*, 2004; Von Broembsen & Kruger, 1985). Consequently, the lack of records of *P. cinnamomi* in regions within the potential distribution range, may be not because of its absence, but because disease

has not been observed within resistant/tolerant vegetation. For example, the regions of Uruguay, southern Brazil and Buenos Aires Province and Turkey, that are climatically suitable for *P. cinnamomi*, are natural grasslands containing species not known to be susceptible (Erwin & Ribeiro, 1996).

Altogether, edaphic factors and vegetation types could explain the lack of occurrence data in regions predicted to be suitable by the CLIMEX model, as the lack of disease symptoms may have precluded the need for testing. The development of pest risk maps on a region scale requires the input of additional information other than climate suitability such as those discussed here; the presence of susceptible hosts and various edaphic factors (Venette *et al.*, 2010). Excellent regional scale models have been developed for other organisms. For example, a CLIMEX model for the distribution of myrtle rust in Australia was modified by including the distribution of hosts in the Myrtaceae (Kriticos *et al.*, 2013). Our CLIMEX model for *P. cinnamomi* provides the base layer for the development of more sophisticated regional distribution models.

Moving forward (potential spread under future climate)

Under the A1B climate change scenario there will be limited potential for spread of *P. cinnamomi* at a continental scale in the tropics and sub-tropics, and also in those regions expected to become drier, such as in the southwest of WA. However, the pathogen may move to higher elevations where there is adequate rainfall. The climate is also projected to become more favourable toward the poles. Thus, the distribution in Canada, Scandinavia, eastern Europe and Japan is likely to expand, and some areas in the southern hemisphere will become more suitable. Previous projections for distribution of *P. cinnamomi* in Europe in a warmer climate (Brasier & Scott, 1994), also projected expansion northwards and eastwards, although they concluded that the pathogen would be unlikely to become significantly active

in areas with cold winters. By examining 40 years of data on *P. alni* in France, Aguayo *et al.* (2014) found both low winter temperatures and hot summers were unfavourable to the disease, and they predicted that future climate change would either enhance or decrease disease severity in Europe depending on the region. The susceptibility of much of the flora in the northern hemisphere is unknown, but known susceptible flora are present in Tasmania (central highlands and mountains), New Zealand (South Island) and Patagonia (Barker *et al.*, 2007; Newhook & Podger, 1972; Podger *et al.*, 1990). That aside, even if a region is projected to become less favourable for *P. cinnamomi* in the future, it does not mean that the pathogen will disappear. In fact, only regions with a projected contraction in potential range due to drying, are likely to see a reduction in pathogen impact, provided this is not coupled with a moist season promoting host infection.

The CLIMEX model is based on the pathogen's biology and distribution and does not account for host susceptibility. Regardless of climate change, susceptible species will still be susceptible and will succumb to even a chance encounter with the pathogen under the right climatic conditions, and plants naturally resistant should remain resistant. The biggest impact of climate change is likely to be on moderately resistant/susceptible or tolerant plants that may normally be able to outpace the pathogen (Thompson *et al.*, 2014). *Phytophthora cinnamomi* can survive as a biotroph and/or endophyte on some native annuals and herbaceous perennial species in the absence of disease symptoms (Crone *et al.*, 2013a; 2013b). In future, these 'symptomless' areas may start to express more disease, as conditions become more conducive to the pathogen and more adverse to the plant species/communities.

A coordinated sampling strategy focussing on natural ecosystems in regions where conditions are projected to be suitable by our CLIMEX model, will allow the distribution to be determined. Roots and soil could be collected at random and, if possible, traditional isolation

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protocols which enable isolate recovery could be conducted. Alternatively, eDNA could be extracted from these samples in a similar manner to the protocol outlined in this study, and the presence of *P. cinnamomi* determined by either HTS or using *P. cinnamomi* specific PCR assays. This sampling would bring even sharper resolution to the projected distribution. Additionally, experimentation on the phenotypic plasticity within *P. cinnamomi* and its ability to adapt to different climatic conditions (e, g. temperature, matric potential) could be implemented to bring a deeper understanding into the biology and underpin future modelling ventures. Specifically, based on the new CLIMEX model we can pose hypotheses on aspects of climate that should be tested, including susceptibility to cold stress and growth in natural environments in relation to warm temperatures.

Conclusions

We have produced a global distribution map for *P. cinnamomi* congruent with existing records. While the pathogen is now widespread, the greatest disease impact is seen where there is the perfect combination of conducive soils, susceptible hosts and ideal climate for disease expression (warm wet winter/spring, followed by dry summer). These are the climatic conditions of the southwest of Western Australia and the Cape region of South Africa, where the greatest impacts are observed in heathlands on nutritionally poor soils, dominated by Proteaceae,. As these climates become drier and warmer, and theoretically less favourable to *P. cinnamomi*, disease expression will still occur because the vegetation is susceptible to the pathogen, but it is expected to decrease in incidence and severity. Other regions, under threat of *P. cinnamomi* invasion under the A1B global warming scenario, are sub-alpine regions in Australia where cold stress has previously restricted disease development together with regions such as Patagonia and the South Island of New Zealand. Much of Canada and Scandinavia will also become suitable for *P. cinnamomi*; however, in

the absence of known susceptible hosts, and because soils are younger and more fertile, the disease impact may be less than in other regions.

Governments and relevant environmental managers can use this CLIMEX model to assess regions at greatest risk to *P. cinnamomi*, in order to coordinate targeted sampling strategies and to implement hygiene and quarantine procedures. This information together with local knowledge on edaphic factors, land use, microclimate, threatened species and vulnerable communities can be used for prioritising management activities.

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Figure Captions

Fig. 1. The historical climate suitability of *P. cinnamomi* based on the NA model is indicated for the world by the CLIMEX Ecoclimatic Index (EI) using climate averages at 10 x 10' resolution from 1961-1990. Positive locality records (open circles) of *Phytophthora cinnamomi*, for six regions of the world, (a) the Pacific coast of North America, (b) Eastern North America, (c) south east Asia, (d) New Guinea, (e) New Zealand, and (f) Argentina and neighboring regions of South America. Negative records (crosses) shown for eastern North America (b). CLIMEX climatic suitability is shown by EI values as indicated by the changing colour scale: unsuitable (EI = 0), marginal (EI = 1-10), suitable (EI = 10-40), optimal (EI > 40). Details for Australia are shown in Fig. 2.

Fig. 2 The historical climate suitability of *Phytophthora cinnamomi* based on the NA model is indicated for Australia by the CLIMEX Ecoclimatic Index (EI) using climate averages at 10 x 10' resolution from 1961-1990 and incorporating cold stress based on North American records. (a) Positive locality records (blue circles) and (b) negative records (green circles) for *Phytophthora cinnamomi*.

Fig. 3 The historical climate suitability of *Phytophthora cinnamomi* based on the NA model is indicated for Australia by the CLIMEX Ecoclimatic Index (EI) using climate averages at 10 x 10' resolution from 1961-1990. Positive (blue squares) and negative (green squares) locality records of *Phytophthora cinnamomi* detected using high throughput sequencing, for (a) southwest Western Australia (b) Tasmania (c) Far North Queensland and (d) Victoria and New South Wales (including a higher resolution insert for the Australian Alps)

Fig 4. Ratio of *Phytophthora cinnamomi* positive to total records for 10x10' cells (Y) in southwest Western Australia (a) and in relation to the Ecoclimatic Index value of each cell (x) (b). The increasing ratio of positive records is shown by increasing circle size (a). Only 10 x 10' cells with 10 or more records are shown (a) and included in the analysis of the logistic regression (b). The average (+ SE) records per cell was 120 + 11.6, range 10 – 1097. $Y=1/(1-e^{-((x-a)/b)})$ a=37.46, b=14.09, $r^2=0.49$, N=224, P<0.001).

Fig. 5. World distribution as given in Fig. 1 plus the projected climate suitability of *Phytophthora cinnamomi*, as indicated by the CLIMEX Ecoclimatic Index (EI) using the CSIRO Mk3 projections for 2080 based on the A1B scenario. Areas where EI will remain zero are in brown while those projected to become unsuitable for the survival of *P.*

cinnamomi are in purple. The projected expansion of climates suitable for *P. cinnamomi* are indicated in green, while areas currently suitable are in blue.

Supporting Information captions

Table S1. Sources of locality data for presence or absence of *Phytophthora cinnamomi*

Table S2. Information sources used to initiate the CLIMEX modelling process in various models.

Fig. S1. The world distribution of the Temperature Index, Moisture Index and Growth Index components of the CLIMEX model

Fig. S2. The world distribution of Cold, Heat and Dry Stress components of the CLIMEX model

Fig. S3. CLIMEX model based on Tasmanian historical records (the TAS model).

Fig. S4. World distribution of *Phytophthora cinnamomi* based on country or region presence or absence based on CABI/EPPO records (Anonymous, 1991).

Fig. S5. Comparison of current and previous CLIMEX models

Fig. S6. Projected climate suitability of *Phytophthora cinnamomi*, as indicated by the CLIMEX Ecoclimatic Index (EI) using the CSIRO Mk3 projections for 2080 based on the A1B scenario.

Fig. S7. World distribution of Ecoclimatic Index where soil pH is pH >7.0.

Data accessibility

Data available from Dryad DOI: [doi:10.5061/dryad.v1jr7](https://doi.org/10.5061/dryad.v1jr7)

Table 1. CLIMEX parameters values used for modelling the distribution of *Phytophthora cinnamomi* based on the temperature and moisture requirements for development. Note that parameters without units are a dimensionless index of available soil moisture scaled from 0 (oven dry) to 1.0 (field capacity).

Index	Parameter	CLIMEX model						Units
		Brasier and Scott 1994	Sutherst <i>et al.</i> , 1999	Desprez - Loustau <i>et al.</i> , 2007 (in roots)	Desprez - Loustau <i>et al.</i> , 2007 (in stems)	NA Model ¹	TAS model ²	
Temperature	DV0 = lower threshold	15	5	8	8	5	5	°C
	DV1 = lower optimum temperature	22	23	22	22	16	16	°C
	DV2 = upper optimum temperature	27	28	32	32	24	24	°C
	DV3 = upper threshold	31	32	34	34	28	28	°C
Moisture	SM0 = lower soil moisture threshold	0.5	0.4	0.4	0.4	0.4	0.4	
	SM1 = lower optimum soil moisture	0.6	0.7	0.7	0.7	0.7	0.7	
	SM2 = upper optimum soil moisture	1.3	1.3	1.3	1.3	1.7	1.7	
	SM3 = upper soil moisture threshold	2	3.0	3.0	3.0	2.5	2.5	
Cold stress	TTCS = cold stress temperature threshold	5		0	2	-3	-3	°C
	THCS = cold stress temperature rate	-0.001		-0.005	-0.100	-0.002	-0.002	Week ⁻¹
	DTCS = cold stress degree day threshold		10	10	10	10	10	
	DHCS = cold stress degree day rate		-0.0007	-0.0001	-0.0001	-0.0001	-	0.0004
Hot stress	TTHS = temperature threshold		30	34	34	32	32	°C
	THHS = heat stress accumulation rate		0.005	0.002	0.002	0.002	0.002	Week ⁻¹
Dry stress	SMDS = dry stress threshold		0.10	0.10	0.10	0.10	0.10	
	HDS = dry stress rate		-0.05	-0.05	-0.05	-0.055	-0.055	Week ⁻¹
Hot dry stress	TTHD = hot dry temperature threshold		32					°C
	MTHD = hot dry moisture threshold		0.05					
	PHD = hot dry stress accumulation rate		0.005					Week ⁻¹

Note: Empty cells indicate unused values (not all parameters need to be included in CLIMEX).

¹ cold stress based on North American distribution

² cold stress based on Tasmanian distribution

Table 2. Numbers of pixels (10 x10') within six CLIMEX models with and without records of *P. cinnamomi* presence in (A) within Australia (B) outside Australia. Model sensitivity is the percentage of known distribution records covered by the model values of Ecoclimatic Index (EI) > 0 and model prevalence is the proportion of the model universe (Australia or outside Australia) estimated to be climatically suitable.

	Pixels without records	Records within unsuitable area	Pixels within suitable area without records	Records within suitable area	Sensitivity (%)	Prevalence
EI values of pixels	EI=0	EI=0	EI>0	EI>0		
Numbers of pixels with/without presence records	Records=0	Records>0	Records=0	Records>0		
(A) Within Australia²						
Brasier and Scott (1994)	22604	74	2060	602	89%	0.11
Sutherst <i>et al.</i> (1999)	22584	118	2080	558	83%	0.10
Desprez-Loustau <i>et al.</i> (2007) in roots ¹	21145	10	3519	666	99%	0.17
Desprez-Loustau <i>et al.</i> (2007) in stems ¹	21635	60	3029	616	91%	0.14
TAS model	22274	22	2390	654	97%	0.12
NA model	22226	16	2438	660	98%	0.12
(B) Outside Australia³						
Brasier and Scott (1994)	417764	74	122539	84	53%	0.23
Sutherst <i>et al.</i> (1999)	484443	90	55860	68	43%	0.10
Desprez-Loustau <i>et al.</i> (2007) in roots ¹	412932	73	127371	85	54%	0.24
Desprez-Loustau <i>et al.</i> (2007) in stems ¹	426795	77	113508	81	51%	0.21
TAS model	472616	44	67687	114	72%	0.13
NA model	460547	16	79756	142	90%	0.15

¹ Desprez-Loustau *et al.* (2007) selected different parameters to produce two models based on predicted growth in roots or soil (see Table 1)

² The total pixels in Australia is 25,340. The total number of pixels with positive records of *P. cinnamomi* is 676.

³ The total pixels for the outside Australia is 540,461. The total number of pixels with positive records of *P. cinnamomi* is 158.







