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Research Papers

The distribution of *Phytophthora cinnamomi* in the Americas is related to its main host (*Persea americana*), but with high potential for expansion

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Summary. *Phytophthora cinnamomi* is among the most destructive plant pathogens that affect many host plants in different ecosystems. Economically important hosts of this pathogen include avocado (*Persea americana*), and this oomycete may cause large-scale destructive epidemics. This study analyzed the potential geographic distribution of *P. cinnamomi* (pathogen) and avocado (host), and distribution of the pathogen in relation to multiple hosts in the Americas. Niche overlap between hosts and pathogen were also evaluated, using a multistep process of ecological niche modelling and the MaxEnt algorithm. Niche similarity among pathogen populations in different hosts and related niche similarity were also examined. As a complement, a tool was designed to visualize the risk of this pathogen in avocado. Results showed that the pathogen was randomly distributed in the avocado niche environmental space, but the niche of the pathogenwas narrower than that of its principal host. The niche of the pathogen was largely a function of the host niches. Areas with potential to grow avocado could present low risk of *P. cinnamomi*, but given the invasiveness of this pathogen, they may be affected in the future.

Keywords. Ecological Niche Model, environment, niche overlap, plant epidemiology, risk maps.

INTRODUCTION

Phytophthora cinnamomi Rands is one of the most important and devastating plant pathogens (Zentmyer, 1980; Bohlen, 2006; Burgess *et al*., 2017; Hardham and Blackman, 2018). This oomycete is known to infect >3000 host plant species, causing disease in orchard and forestry species. It has the potential to occupy a broad geographic distribution, due to its genetic plasticity under different environmental conditions (Zentmyer, 1980; Burgess *et al*., 2017; Hardham and Blackman, 2018; Ramírez-Gil and Peterson, 2019). This pathogen causes root rot of avocado (*Persea americana* Mill), which is

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the most serious disease of avocado in the most countries where this crop is grown (Zentmyer, 1980; 1984; Ramírez-Gil *et al.*, 2017; Hardham and Blackman, 2018).

Phytophthora cinnamomi is reported from tropical and subtropical zones and from many different ecosystems, where it may cause severe diseases on crops and wild plants (Pratt and Heather, 1973; Weste and Marks, 1974; Zentmyer, 1997; Duque-Lazo *et al.*, 2016; Burgess *et al.*, 2017; Hardham and Blackman, 2018; Ramírez-Gil and Peterson, 2019). Zentmyer (1997) reported that *P. cinnamomi* had not been recovered from any native trees growing at undisturbed sites in America, suggesting that it is not a native pathogen of these plants. This is supported by this pathogen having scattered distribution, and by the high susceptibility of America's native flora (Weste and Marks, 1974). The scattered distribution is likely to be the result of different introduction histories of the pathogen. *Phytophthora cinnamomi* could have been introduced into America by human-mediated movement, probably from Southeast Asia (Zentmyer, 1988, 1997; Socorro-Serrano *et al.*, 2019) .

Avocado is one of the most economically important hosts of *P. cinnamomi* (Zentmyer, 1980; Ramírez-Gil *et al.*, 2017; Hardham and Blackman, 2018). The centre of origin of *P. americana* is tropical America (GalindoTovar *et al.*, 2008). This fruit tree is the most important cultivated species in *Lauraceae* (Schaffer *et al.*, 2013), and includes three botanical races: Mexican (*P. americana* var. *drymifolia*), Guatemalan (*P. americana* var. *guatemalensis*), and West Indian (*P. americana* var. *americana*) (GalindoTovar *et al.*, 2008). Hybridization among races has generated great phenotypic variability, and avocados are now grown under diverse environmental conditions, including semiarid Mediterranean, subtropical, and tropical climates (Papadakis, 1966; Knight and Campbell, 1999; Chen *et al.*, 2009; Bost *et al.*, 2013).

Ecological niche models (ENMs) relate known occurrence of species to environmental variation, to determine the ecological requirements of species. Based on those requirements the potential geographic distribution of such species can be estimated (Peterson *et al.*, 2011). ENMs may have diverse practical applications in agriculture, including prediction of geographic distribution of economic crops and their pest and diseases, modelling of productivity, assessment of the potential for biological invasions by insects, weeds and pathogens, and forecast climate change impacts (Meyer *et al.*, 2010; Burgess *et al.*, 2017; Narouei-Khandan *et al.*, 2017; Ramírez-Gil *et al.*, 2018; Johnson *et al.*, 2019; Ramírez-Gil and Peterson, 2019). Another application of ENMs is assessment of niche similarity among different species to establish whether those niches are different or have diverged (Maher *et al.*, 2010; Qiao *et al.*, 2017).

ENMs have been used to determine the potential distribution of *P. cinnamomi* in natural ecosystems (Duque-Lazo *et al.*, 2016; Burgess *et al.*, 2017; Hernández-Lambraño *et al.*, 2018; Sena *et al.*, 2019), and at a regional level in avocado crops (Ramírez-Gil and Peterson, 2019). However, no study evaluating naturally distributed and cultivated *P. cinnamomi* hosts has been reported across the Americas. The present paper reports the application of ENM approaches to provide understanding of how the potential geographical distribution of native and commercially cultivated avocado genotypes and *P. cinnamomi*, varies across the Americas. Ecological niches of *P. cinnamomi* in different plant hosts were also estimated and compared.

MATERIAL AND METHODS

Occurrence and environmental data

Records (15,560) associated with commercial avocado varieties in production fields (cultivars including: Hass, Fuerte, Reed, Zutano, Gottdried, Semil, Ettinger, Bacon, Hall, Lula, Collinred, Edranol, Lorena, Trapp, Booth, Choquette, and Trinidad), and native avocado genotypes related to the three races in natural ecosystems (*P. americana* var. *drymifolia*, *P. americana* var. *guatemalensis*, and *P. americana* var. *americana*). The records were obtained from Argentina, Brazil, Chile, Peru, Ecuador, Colombia, Panamá, Costa Rica, Cuba, Dominican Republic, El Salvador, Haiti, Honduras, Puerto Rico, Trinidad and Tobago, Guatemala, Mexico and the United States of America (USA; California and Florida). Data were obtained from different ecological conditions in a wide range of altitude (0 to 3200 m above sea level). Details about the origins of data and how they were obtained are described in Supplementary Information 1. Each data point was corroborated by visual inspection in Google Earth (accessed 3 March 2017), eliminating 2,503 sites that clearly did not correspond to avocado fields, or that were duplicated. Effects of spatial autocorrelation in data occurrence were reduced using 4.5 km distance filtering in the SDMtoolbox implemented in ArcGis (ESRI ™) (Brown, 2014), leaving a final set of 1,286 occurrence records for further analyses (Figure 1 A). The criterion for selecting this distance was determined based on the spatial resolution of the predictive variables (i.e., bioclimatic variables; see following paragraphs).

Occurrence data for *P. cinnamomi* on different hosts were obtained from published reports, databases, websites including the Global Biodiversity Information

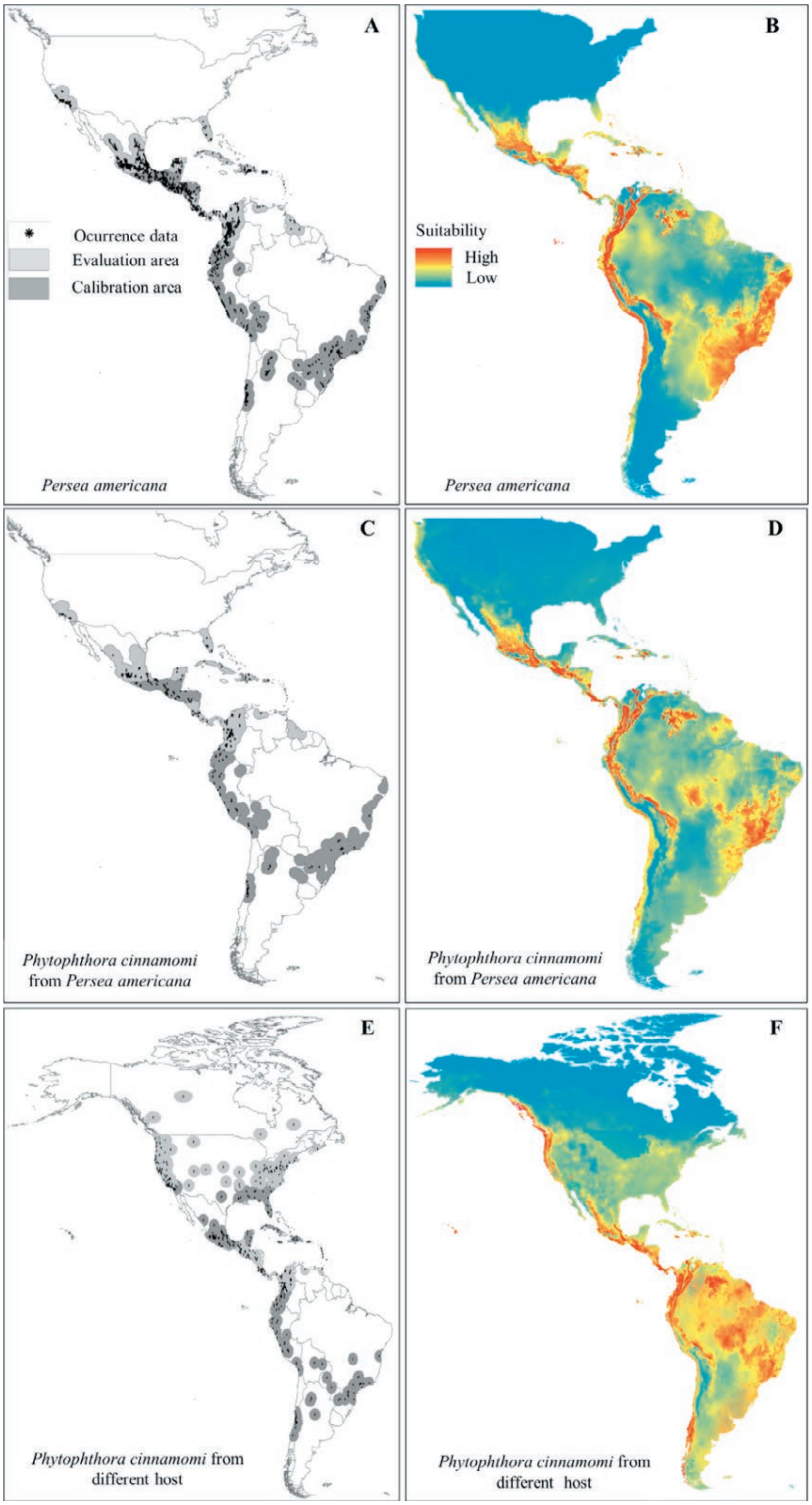

Figure 1. Potential distributions of *Persea americana* and *Phytophthora cinnamomi* under present environmental conditions in North and South America. Model calibration and evaluation areas (dark and light grey), and presence (black dots) data, documenting occurrences *Persea americana*, *Phytophthora cinnamomi* from *Persea americana*, and *P. cinnamomi* from hosts different to avocado (A, C, and E). Potential distribution of *P. americana*, *P. cinnamomi* from *P. americana*, and *P. cinnamomi* from all hosts (B, D, and F) under current environmental conditions in America. The map is the median of the logistic suitable index across the 10 replica models reported in Table 1.

Facility (GBIF; www.gbif.org), Invasive Species Compendium (https://www.cabi.org/isc/datasheet/40957), Center for Invasive Species and Ecosystems Health (https://www.invasive.org/species.cfm), Forest Phytophthoras of the World (http://forestphytophthoras.org/species/cinnamomi/disease), Plantwise Knowledge Bank (https://www.plantwise.org/knowledgebank/#.), and individual researchers (see Supplementary Information 1 for a list of sources for each country). A total of 206 records were collected from avocado, from across Latin America and the USA , and 194 additional records collected from other hosts distributed across the Americas, including four records from Canada (Figure 1, C and E). The criteria described above were applied to each of presence (i, corroborating that the coordinates were associated with the reported region, ii, removing duplicates, and iii, reducing spatial autocorrelation (4.5 km distance filtering)). The final data consisted of 205 records from avocado and 192 from other hosts (Figure 1, C and E).

All presences of *P. cinnamomi* from avocado, from different hosts; and from *P. americana* were randomly divided into four groups, each with equal numbers according to latitude (Figure 1, A, C and E), where 50% was used for calibration and the other 50% for evaluation of the models.

As environmental predictors, the bioclimatic variables available from the WorldClim climate data archive (Hijmans *et al.*, 2005) were initially used. The variables bio 8 (Mean Temperature of Wettest Quarter), 9 (Mean Temperature of Driest Quarter), 18 (Precipitation of Warmest Quarter), and 19 (Precipitation of Coldest Quarter) were eliminated *a priori*, due to known spatial artifacts in these data layers (Escobar *et al.*, 2014). All analyses were conducted at a spatial resolution of 2.5' (approx. 4 km^2), as a balance between obtaining sufficient spatial detail and avoiding excessive computational load and storage demands. Climate data sets were masked to temperate and tropical America, excluding Canada, Alaska, and small Caribbean islands, for avocado and *P. cinnamomi*-infected avocado data. In addition, the predictive analysis was extended to all America including data of *P. cinnamomi* from hosts different to avocado.

Ecological niche modelling

Three ecological niche models (ENMs) were developed. The first was for avocados (including commercial varieties and native genotypes associated with the three botanical races). The second model was for *P. cinnamomi* that was reported infecting avocado (Supplementary Information 1). The third model was for *P. cinnamomi* infecting hosts different from avocado in the Americas (Supplementary Information 1). ENMs were based on the maximum entropy algorithm implemented in Maxent version 3.3.3k (Phillips *et al.*, 2006).

Three steps were used for the development of ENMs with the best predictive ability. The first was definition of a calibration area as the area accessible to the species of study over a relevant period (termed M) (Barve *et al.*, 2011; Saupe *et al.*, 2012). M was selected as all land areas within 100 km^2 for avocado presence, within 150 km^2 for *P. cinnamomi* from avocados, and within 200 km^2 for *P. cinnamomi* from different hosts to avocado. This was based on potential areas of influence of *P. cinnamomi* and its hosts (Figure 1, A, C, and E). For the second step, the best set of environmental predictors for our models was selected using jackknife routines in Maxent software. The third step used model selection approaches to optimize parameter settings in Maxent, based on Akaike Information Criterion (AIC$_c$) values calculated using ENMTools version 1.3 (Warren *et al.*, 2010), from models calibrated with 50% of input points (all calibration points that corresponded to 50% of all presences), ten cross-validated replicates, and raw model outputs. Combinations were evaluated of the regularization multiplier (β) (0.25, 0.5, 1, 1.5, 2, 4, 6, 8 and 10), response types (L, LQ, LQP, LQPT, and LQPTH; where L = linear, Q = quadratic, P = product, T = threshold, and H = hinge), and the six sets of environmental variables (the climatic variables 5, 7, 9, 11, 13, and 15) using jackknife routines as described above. In total 270 models were evaluated.

To assess the robustness and predictive ability of the obtained models, three groups were selected based on the AIC$_c$ values for each of the target taxa (Figure 1), that showed the least, medium and greatest AIC$_c$ values, but with different parameter settings and environmental data layers (for details, the summary of the total models evaluated in Table 1). For each of the ENMs, four sub-regions were created with approximately equal numbers of occurrences, by dividing the region according to latitude. The sub-regions were: 1 (south of Colombia, Ecuador, Peru, Bolivia; Brazil, Paraguay, Uruguay, Argentina, and Chile); 2 (north of Colombia, south of Central America and the Caribbean islands); 3 (north of Central America, south of Mexico, and north the Caribbean islands; and 4 (north of Mexico, California, Florida; USA, and part of Canada) (Figure 1, A, C, and E). Maxent was then used with ten cross-validated replicates and logistic output format. For this stage of analysis, sub-regions 1 and 3 were used for calibration, and subregions 2 and 4 were used for evaluations (Figure 1, A, C, and E).

Model quality was evaluated based on complexity, using AIC$_c$ values (above), and the significance of predictions based on partial receiver operating characteristic (partialROC) approaches (Peterson *et al*., 2008). Functions used are available in Niche Toolbox (http://shiny.conabio.gob.mx:3838/nichetoolb2/). An acceptable omission rate of $E = 5\%$, and bootstrap analysis with 1000 iterations were used, with random subsamples of 50% of each dataset tested for each of the generated models. The probability associated with the test was determined by direct count of replicates in which the partial ROC statistics was ≤ 1. Performance was evaluated with the omission rate (OR) calculated via thresholding models of the calibration sub-regions, based on the greatest model output value that was associated with $\leq 5\%$ omission of calibration data. Once this threshold was imposed on the other sub-regions, OR was calculated based on the evaluation data.

The best models from the three data groups (avocado, *P. cinnamomi* from avocado), and *P. cinnamomi* from different hosts to avocado, were chosen considering, firstly, significance (partial ROC), then performance (OR < 6.2%), and lastly, the minimum complexity (lowest values of AICc), in that order (Table 1). Next, only models within 2 units of the minimum AICc values were retained. These models were then projected across temperate and tropical America, excluding Canada, Alaska, and small Caribbean islands, for avocado and avocado infected with *P. cinnamomi*, but all America was included for *P. cinnamomi* from different hosts to avocado, using Maxent with no clamping or extrapolation, and with ten bootstrap replicates and logistic outputs.

Niche similarity

To assess whether *P. cinnamomi* has an ecological niche distinct from that of its avocado host, a resampling exercise was carried out from the presences of avocado (native and commercial genotypes) in the Americas associated with the occurrence of this species under different environmental conditions (edaphic properties, climatic, topographic, or biophysical variables), contrasting anthropic conditions (agronomic management practices, culture), and genetic variability. One hundred random combinations were drawn of avocado occurrence points to mimic 204 infected points (described above) that were available, using our code in R (R Development Core Team, 2021). For each point, values were extracted that were associated with the environmental variables coinciding in the selection of the ENMs of avocado and *P. cinnamomi* described above (bio 1, 5, 10, and 12. Table 1), and frequency histograms were made of means among these null replicates. The actual mean and standard deviation values observed for known occurrences of *P. cinnamomic* were then compared. This test was designed to assess whether the pathogen (*P. cinnamomi*) had a niche distinct to that of its economic host of study (avocado).

NicheA was used for the visualization of niche overlap based on minimum volume ellipsoids for the species in three PCA dimensions (Qiao *et al*., 2016), considering the climatic variables that the three models had in common (bio 1, 5, 10, and 12. Table 1). Subsequently, this analysis was complemented with the Jaccard index (I_J), as a numerical metric of environmental overlap between the two species studied (Jaccard, 1912; Qiao *et al*., 2017).

Risk visualization of Phytophthora cinnamomi in avocado in the Americas

To determine the risk of *P. cinnamomi* in avocado (cultivated varieties and native races) in the Americas, the outputs of the ENMs from avocado, *P. cinnamomi* from avocado, and *P. cinnamomi* from other hosts were used to determine three areas. These were: (i) areas with avocado with current distribution of *P. cinnamomi*, obtained as the interception of current distribution of avocado and *P. cinnamomi* from avocado (current risk, represented in yellow); (ii) areas with current and potential avocado that could become infected by *P. cinnamomi* in the future, obtained as the current and potential distribution of avocado, which are not related to the *P. cinnamomi* distribution from avocado, but which can be potentially affected with *P. cinnamomi* potential distribution associated with other hosts (potential risk, represented in red); and (iii) areas with avocado that are not suitable to *P. cinnamomi* based on all ENMs from *P. cinnamomi* (low risk, represented in green). The visualization map of the risk of *P. cinnamomi* was made. the three model transfers were reclassified to binary (0 and 1) with a threshold determined on calibration areas as described above, applied to the median value of the ten replicates. Later, we summed these grids to produce a layer with values from 0 to 3 (values with 0 = no host; values with 1 = low risk; values with 2 = potential risk; values with 3 = current risk). The current, potential and low risk in these results were visualized using a grid combination approach (Ramírez-Gil *et al*., 2019).

RESULTS

Model selection

The three parameters that were explored in selection of the model (features, β regularization multiplier, and the combination of environmental variables) generated a set of candidate models for further assessment. The best models were selected using these parameters, considering as criteria a prediction capacity greater than random ($P < 0.001$), models with the lower complexity (lower AIC value), and good performance based on low omission rate values (Table 1). As a result, the models with better behaviour for *Persea americana*, *P. cinnamomi* from avocado and *P. cinnamomi* from different hosts to avocado were related to the features responses of the MaxEnt algorithm of quadratic (LQ), quadratic (LQ), and product (LQP) type, with a set of combination of 6, 6, and 7 bioclimatic variables, and β regularization multiplier of 2, 1.5 and 4, respectively. In general, models with high numbers of predictive variables (≥ 9), low or high β regularization multiplier (≤1 and >4) and threshold (LQPT) and hinge (LQPTH) features, showed lower metrics that are desirable for a better model (significance, performance, and complexity) (Table 1)

Geographic distributions

The projection of ENMs for avocados (commercial varieties and native genotypes) indicated that this species shows a wide distribution across the Americas. High-suitability areas were associated with the Valleys of California in the USA, a wide region from central and southern Mexico, parts of Central America distributed in Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica and Panama, small areas in the Caribbean Islands including Southern Cuba, Jamaica, Dominican Republic, Haiti, Puerto Rico, and the Guianas, the highlands of Colombia, Ecuador, Peru, Bolivia, and Venezuela, the Caribbean and Pacific coasts of Colombia and Venezuela, the coastal valleys of Peru and Chile, the Amazonian portion located in the south of Venezuela and the north of Brazil and the southeastern and northeastern coasts of Brazil (Figure 1 B). These results suggested new areas that can be used for planting (potential crops) or by natural expansion (potential areas with natives races). These areas are localized in the South (Brazil, Argentina, Chile, Bolivia, Paraguay, and Uruguay), and North (Mexico and USA) (Figure 1 B). The

Table 1. Description of selected models and corresponding parameters based on the Maxent algorithm.

Target taxa	AIC_c[1] classification	Features[2]	β (regularization multiplier)	Bioclimatic variables	AIC to calibration models[1]	Projected parameters		
						pROC[3]	OR[4]	AICc[1]
Avocado	High	LQPTH	4	1, 3, 4, 5, 6, 10, 12, 14, 15, 16 and 17	1203,431	0.001	5.3	948,609
	High	LQPT	6	1, 3, 4, 5, 6, 10, 12, 15, and 16	1125,101	0.001	6.8	821,319
	Medium	LQPT	4	1, 3, 4, 5, 6, 10, 12, and 15	836,108	0.001	7.3	763,815
	Medium	LQP	2	1, 4, 5, 6, 10, 12, and 16	828,436	0.001	6.8	656,414
	Low	LQP	1.5	1, 4, 6, 10, 12, and 12	718.607	0.001	6.3	648,602
	Low[a]	LQ	2	1, 4, 5, 6, 10, and 12	708,500	0.001	5.8	508,135
P. cinnamomi from avocado	High	LQPTH	4	1, 4, 5, 7, 10, 12, 13, 14, 15, and 16	2301,351	0.001	5.0	1022,452
	High	LQPTH	2	1, 4, 5, 7, 10, 12, 13, 14, and 16	2009,913	0.001	5.3	1211,489
	Medium	LQPT	4	1, 4, 5, 7, 10, 12, 13, and 16	1758,933	0.001	6.8	843,611
	Medium	LQPT	6	1, 4, 5, 7, 10, 12, 13, and 16	1686,231	0.001	5.9	742,981
	Low	LQ	2	1, 4, 5, 10, 12, 13, and 16	1181.607	0.001	5.2	535,142
	Low[b]	LQ	1.5	1, 5, 10, 12, 13, and 16	1011.117	0.001	4.8	505,171
P. cinnamomi from different hosts	High	LQPTH	6	Bio 1, 4, 5, 7, 10, 12, 13, 14, 15, 16 and 17	1985,419	0.001	3.8	928,318
	High	LQPTH	6	Bio 1, 4, 5, 7, 10, 12, 13, 14, 15, and 16	1871,123	0.001	4.2	895,223
	Medium	LQPT	4	Bio 1, 4, 5, 7, 10, 12, 13, 14, and 16	1421,413	0.001	6.4	712,156
	Medium	LQP	2	Bio 1, 4, 5, 7, 10, 12, 13, and 16	1385,142	0.001	6.8	623,412
	Low	LQ	1	Bio 1, 5, 7, 10, 12, 13, and 14	816.101	0.001	6.7	518,201
	Low[c]	LQP	4.0	Bio 1, 5, 7, 12, 13, and 16	745.221	0.001	6.2	507,013

[1] AICc: Akaike information criterion.

[2] Quadratic (LQ), product (LQP), threshold (LQPT), and hinge (LQPTH).

[3] Significance (P value).

[4] Omission rate (%).

[a,b and c] Model selected for analyses of, respectively, potential distributions of avocado, *P. cinnamomi* from avocado and *P. cinnamomi* from different hosts.

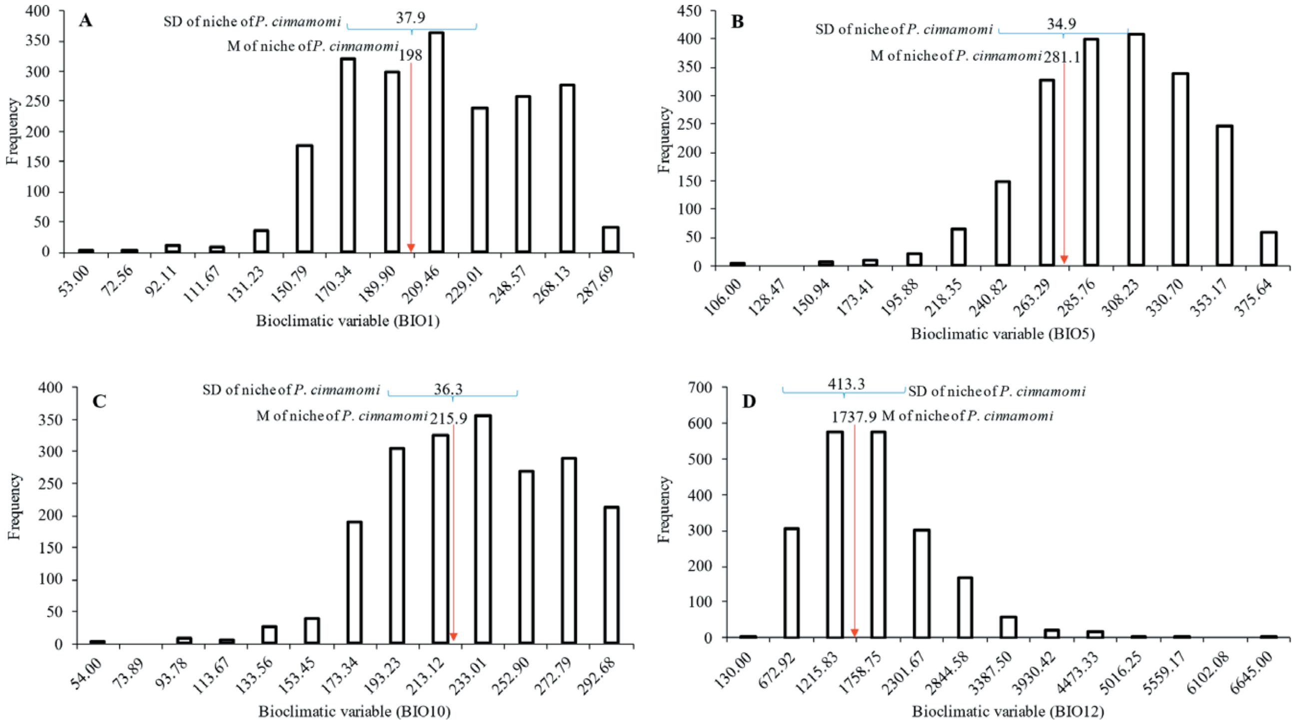

Figure 2. Relationship between coincident bioclimatic variables of the ecological niche models of *Persea americana* and *Phytophthora cinnamomi* from *Persea Americana*. A: BIO 1: Annual Mean Temperature. B: BIO 5: Maximum Temperature of Warmest Month. C: BIO 10: Mean Temperature of Warmest Quarter. D: BIO 12: Annual Precipitation. The values on the blue lines represent the standard deviations (SD), and the red down arrows represent the median (M) of the variables obtained for the niche of *Phytophthora cinnamomi* obtained records from *Persea americana*. Black bars represent the frequency values of the variables for the niche of *P. americana* under Americas. All variable values were obtained from 100 random combinations of occurrence (*Phytophthora cinnamomi* and *Persea americana*) and extracted from the niche of *Phytophthora cinnamomi* and *Persea americana* under Americas distributions.

potential distribution of *P. cinnamomi* isolated from avocado was very similar to that of avocados, although with a smaller overall area. In this model, *P. cinnamomi* suitability was more restricted in the central zone and southeastern and northeastern coasts of Brazil, with lower suitability in the coastal valleys of Peru and Chile. Suitable areas were also reduced in the Caribbean islands. A suitable region was also identified in the centre of Brazil (eastern Mato Grosso) (Figure 1 D).

The ENM for *P. cinnamomi* from hosts other than avocado showed a broader distribution than the other two models (Figure 1 F). The range included areas across much of the Americas and low suitability only in Canada and Alaska. The Amazonian region showed the greatest suitability values, together with the Pacific region of Colombia and Ecuador, the Andean regions from Colombia to Peru, and parts of Chile, Central America, and the Caribbean. Similarly, median suitable zones were noted in parts of Mexico, and the USA. The regions with the lowest suitability for the infection of *P. cinnamomi* were desert regions and some temperate areas (Figure 1 F).

Niche overlap

The initial analysis to compare niches of avocado and *P. cinnamomi* isolated from avocado showed that the mean of occurrences of *P. cinnamomi* was close to that of the null distribution, suggesting that *P. cinnamomi* is randomly distributed within the avocado niche (Figure 2). The Jaccard index indicated an environmental overlap of 0.68 between *P. americana* and *P. cinnamomi*, whereas for *P. americana* and *P. cinnamomi* associated with hosts other than avocado the overlap was of 0.75, and for *P. cinnamomi* isolated from avocado and *P. cinnamomi* isolated from hosts different to avocado the overlap index was 0.58 (Figure 3).

Comparison between niches based on a model of minimum-volume ellipsoids of *P. americana* and *P. cinnamomi* isolated from avocado showed that the latter was narrower than the former. When the three niches were compared, the niche of *P. cinnamomi* generated from different hosts including avocado (in Table 1) was the widest of all (Figure 3).

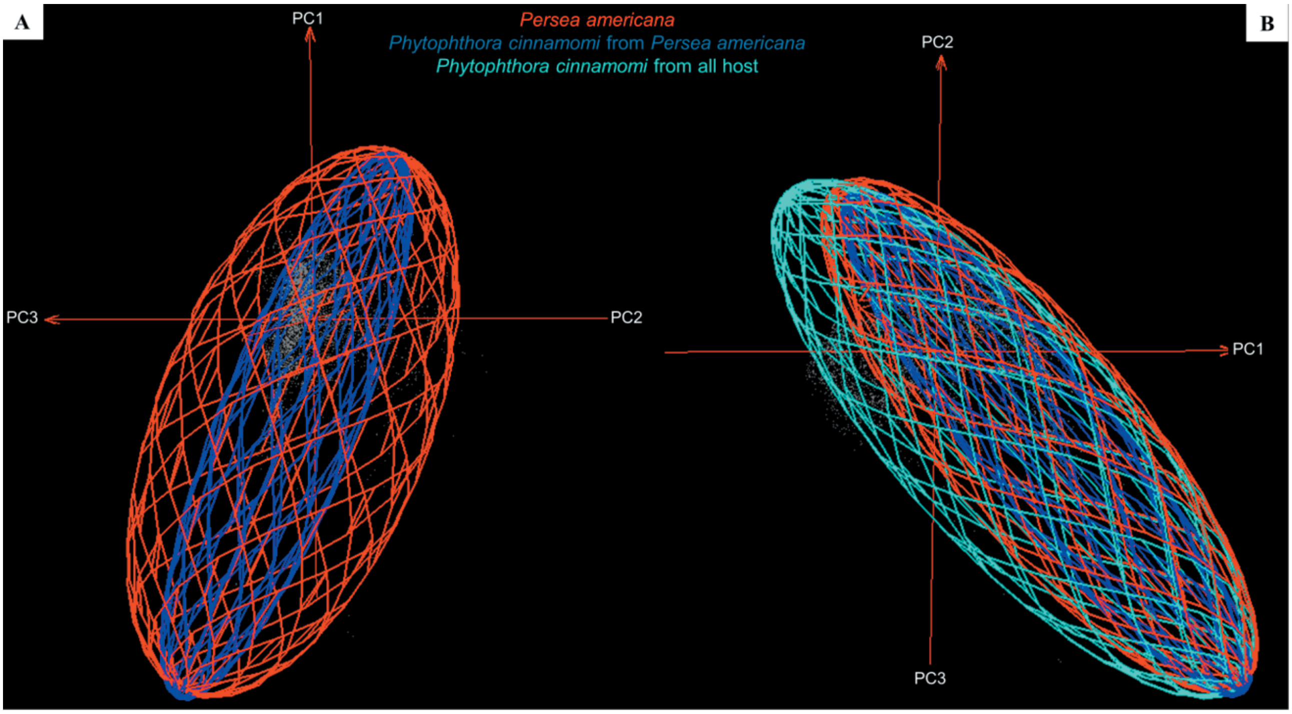

Figure 3. Environmental space of *Persea americana*, *Phytophthora cinnamomi* from *P. americana* (A), and *P. cinnamomi* from different hosts (B), modeled in NicheA. Ecological niche models based on a model of minimum-volume ellipsoids and visualization in three dimensions associated with principal component of bio-variables (Table 1). PC: principal components.

Risk visualization of Phytophthora cinnamomi *in avocado in the Americas*

Three zones with differential risk associated with *P. cinnamomi* were generated in cultivated and native avocados in the Americas (Figure 4). The low risk zone (green), was areas in which there are reports of the presence of *P. cinnamomi* and its main host (avocado), but where conditions for establishment of the pathogen are low, without being null. These areas could have potential for the development of this host without strong pressure from its main pathogen (Figure 4). The current risk zone (yellow), was for places where the conditions for the development of the host and the pathogen are ideal (niche overlap). In these areas root rot occurs continuously with different levels of intensity, which are highly dependent on climatic variations and the stability of the ecosystem (Figure 4). The potential risk zone (red), are areas where the environmental conditions for development of the host are suitable (potential distribution), but which presents current distribution of the pathogen, associated with other hosts. These zones would be restrictive for avocado, given high probability of being infected by the pathogen that causes its most limiting disease (Figure 4).

Figure 4. Risk visualization of *Phytophthora cinnamomi* on avocado (cultivated and native races) in the Americas.

DISCUSSION

Model selection

In recent years the use of ENMs has increased due to their multiple applications (Cobos *et al.*, 2019). These include determination of ecological niches and exploration of potential species distributions (Peterson *et al.*, 2011). Different strategies were used in the present research with the objective to carry out adequate prediction of the ENM and use of the algorithms for its calculation: (i) to clean and reduce the spatial autocorrelation of data occurrence (Varela *et al.*, 2014); (ii) to define an appropriate M, which is based on knowledge of the species to be modelled (Barve *et al.*, 2011; Saupe *et al.*, 2012); (iii) to reduce the dimension of environmental variables, eliminating those with lower prediction capacity (Varela *et al.*, 2014); and (iv) to carry out a strict selection process of criteria for the algorithms used (Warren and Seifert, 2011; Radosavljevic and Anderson, 2014; Ramírez-Gil *et al.*, 2018; Cobos *et al.*, 2019; Ramírez-Gil and Peterson, 2019). Rigour applied in this study gave a robust and reliable framework for the analysis performed, as shown by the sound results obtained.

Geographic distribution and overlapping of niches of Persia americana, Phytophthora cinnamomi *isolated from avocado, and* P. cinnamomi *isolated from hosts other than avocado*

The potential distributions generated for *P. americana* achieved a good approximation to the actual geographical distribution of this species. This fruit tree is found in a wide area in the Americas, including Latin America from Mexico to Chile which is an important diversification centre of this species (GalindoTovar *et al.*, 2008; Chen *et al.*, 2009; Bost *et al.*, 2013; Schaffer *et al.*, 2013). This wide range may be due to the existence of three races, which hybridized generating multiple genotypes adapted to different ecological and environmental conditions. The West Indian race is predominantly adapted to low lands (below 1000 m altitude), with high temperatures and high humidities. The Guatemalan race is present mainly at intermediate altitudes (1000-2000 m altitude). The Mexican race grows greater altitudes (>2000 m) in the tropical highlands and sub-tropical climates, which are characterized by relatively low temperatures (Bost *et al.*, 2013; Schaffer *et al.*, 2013).

In addition to the avocado natural races and genotypes, many commercial varieties have been developed, possibly increasing the geographical distribution of this species. This has allowed successful cultivation of avocado in a number of regions different from the centre of host origin, including the dry regions of Chile, Peru, Spain, Israel, South Africa and California in the USA, where agronomic practices such as irrigation have been incorporated into the production systems. Avocado use by native Americans was well known before introduction to other continents. Avocado propagation was probably carried out using seeds produced from plant sexual reproduction, which would have resulted in genetic diversity and adaptation of many genotypes (Chen *et al.*, 2009). Therefore, before being cultivated as monocultures, avocado dispersion by humans was probably from a genetically diverse background. This assumption may explain the wide avocado presence and adaptability observed in the present results.

This study indicated that the Americas include many new areas that support avocado crops under anthropic practices (potential crops) or by natural expansion (potential areas of natives races). The present model outputs should be interpreted with some caution, because some of the areas identified as suitable for avocado are unlikely to be profitable and viable (Ramírez-Gil *et al.*, 2019). In addition, commercial varieties may have implicitly incorporated agronomic components (e.g., irrigation systems, drainage, use of fertilizers, planting techniques). Many areas can also be natural reserve zones, deserts, or other regions where agriculture cannot be implemented (Ramírez-Gil *et al.*, 2019). These factors may introduce bias for the analysis of distributions found in the present study. Therefore, caution should be taken when making conclusions from the data obtained.

The potential geographical distribution of *P. cinnamomi* was strongly influenced by host presence, because niche amplitude varied according to the host number considered for its ENM development. The niche of *P. cinnamomi* generated from *P. americana* was only randomly distributed inside the niche of this host, whereas its amplitude increased when other host presences different to avocado where included in the analyses. Evidence suggests that *P. cinnamomi* was probably introduced to America from Asia (Zentmyer, 1988, 1997; Socorro Serrano *et al.*, 2019). Reproduction of *P. cinnamomi* is mainly asexual generating different clonal lineages as primary sources of human-mediated movement between regions (Pagliaccia *et al.*, 2013; Socorro Serrano *et al.*, 2019). Unlike other regions such as Australia, the *P. cinnamomi* host range in America is mostly unknown, but is mainly wild species (Shearer *et al.*, 2004; Hardham and Blackman, 2018). In most regions of America, research has been focused on commercial crops such as avocado, rather than on natural ecosystems such as the Amazon or Pacific rainforest of Colombia and Ecuador, which the present research has indicated are regions with high suitability for *P. cinnamomi*.

Many factors determine pathogen dispersion once introduced in a region. *Phytophthora cinnamomi* has a complex (and controversial) lifestyle, varying from saprophytic to hemibiotroph pathogenic, depending on edaphoclimatic conditions and host availability (Hardham and Blackman, 2018). With exception of made for some regions such as California (USA) and Mexico, the population genetic structure of this important pathogen is unknown in hosts other than commercial crops in most regions of America (Pagliaccia *et al.*, 2013; Socorro Serrano *et al.*, 2019). The saprophytic lifestyle of *P. cinnamomi* has been widely reported (Duvenhage and Kotze, 1991). However, this behaviour has been questioned with results that suggest that *P. cinnamomi* does not behave as a saprophyte, at least under non-sterile soil conditions (McCarren, 2006). If true, this supports the present results, and the hypothesis that the distribution of *P. cinnamomi* follows host distribution but is random with respect to metrics defining the avocado ecological niche, mostly because its current distribution at the long and medium ranges (i.e. the range resolved by the present modelling) is the result of human-mediated introductions rather than natural spread of the pathogen.

A single factor can not explain the current distribution for *P. cinnamomi* in America. Once introduced in a new environment, a microorganism largely depends on the interactions between genetics and environment (Garbelotto, 2008; Burgess *et al.*, 2017). The Americas extensive ecosystem variability, suggesting high adaptability in *P. cinnamomi.* The present results do not allow precise determination of the contribution of each independent factor to current distribution of the pathogen. However, and despite a lack of sound basic biological information on this oomycete, it is tempting to speculate that its current distribution in the Americas has resulted from high adaptability to different environments, following host availability. It has been observed, for example, in Colombia in tropical conditions as a pathogen of hosts growing from 0 to ≈3000 m above sea level, in different ecosystems and edaphoclimatic conditions, from dry tropical dry forests to very humid or pluvial forests (Figure 1).

Despite being suitable for *P. cinnamomi,* there were areas where the pathogen has not been recorded. This may be explained by lack of research particularly on wild plant species, the presence of pathogen suppressive soils in some places, host resistance or host absence, and especially lack of human-mediated introduction pathways. In contrast, *P. cinnamomi* was identified in dry or semi-arid regions which are not suitable for its development. However, these records were mainly on commercial cultivated hosts, where agronomic practices (e.g. irrigation) provide suitable conditions for *P. cinnamomi* development. These conditions could generate bias in determination of distribution areas using the ENMs approach, associated with dependence of presences on the frequency of environmental conditions that occur across geographical space (Broennimann *et al.*, 2012).

Phytophthora cinnamomi has a very broad host range (Hardham and Blackman, 2018). Since this pathogen causes severe losses in several crop types, more knowledge is required about host recognition, pathogenicity determinants and environmental factors that favour disease development under different edaphoclimatic and biological conditions where disease has been reported (Hardham and Blackman 2018). Genome sequencing has demonstrated many genes encoding effector proteins, which may help to explain the wide adaptability to different hosts observed for *P. cinnamomi* (Garbelotto, 2008; Hardham and Blackman, 2018).

This may indicate why the niche of *P. cinnamomi* has increased amplitude when host occurrences other than avocado were included in the analyses. From previous and the present results, it is apparent that *P. cinnamomi* strains have a large niche independently of the host of origin, suggesting that this is a pathogen that does not show strong host preference. In addition, Serrano and Garbelotto (2020) showed that *P. cinnamomi* can infect and cause diseases on hosts other than those from which it was isolated, confirming the broad host range of the pathogen. However, they also presented evidence of host specialization (i.e., some isolates were more aggressive on the hosts they were isolated from) and increased virulence of pathogen genotypes that had no history of coexistence with natural host populations. This may have resulted from lack of co-evolution, or could be the outcome of using highly virulent isolates. Further research is required to determine which of these explanations is correct.

Despite the fact that *P. cinnamomi* distribution was strongly influenced by host presence, other factors may determine distribution of the pathogen and extent of damage it causes (Burgess *et al.*, 2017). Humid regions were more favourable for *P. cinnamomi*, such as the Amazon, the Colombian and Ecuadorian Pacific, regions X and XI in Chile, wide areas in Central America and Mexico, and the Pacific coast of the USA. In contrast, presence of *P. cinnamomi* was affected in low precipitation regions such as the coastal valleys of Chile and Peru. High precipitation increases soil humidity inducing episodes of hypoxia or anoxia, which, in turn, intensifies pathogen aggressiveness. This increases *P. americana* susceptibility in the soil, affecting root functionality

(Stolzy *et al.*, 1967; Sterne *et al.*, 1977; Gisi *et al.*, 1980; Zentmyer, 1984; Sanclemente *et al.*, 2013; Ramírez-Gil *et al.*, 2017; Ramírez-Gil and Morales-Osorio, 2018). Alteration of natural ecosystems may increase aggressiveness of *P. cinnamomi* and, therefore, increase the possibility of root rot epidemics (Zentmyer, 1988, 1997). Most avocado crops are based on clonal genotypes susceptible to *P. cinnamomi*, including 'Hass', which is the main cultivar grown for fruit export. This narrow genetic background may facilitate *P. cinnamomi* dispersion worldwide. Crop production in general is an ecosystem alteration that may induce severe root rot epidemics.

When *P. cinnamomi* is established in an ecosystem, the factors that most determine its distribution are associated with the presence of susceptible hosts (Pratt and Heather, 1973; Duque-Lazo *et al.*, 2016; Ramírez-Gil and Peterson, 2019; Sena *et al.*, 2019). Additionally, other factors such as humidity, temperature, soil water movement, and nutrient availability are associated with its aggressiveness, and are known as disease conductive variables (Corcobado *et al.*, 2013; Ramírez-Gil and Morales-Osorio, 2018). There are other parameters not included in the present research that may be related to the distribution and establishment of *P. cinnamomi* ecosystems or agroecosystems. These include degrees of host susceptibility, anthropic management practices, dispersal mechanisms, conductive factors, and degrees of ecosystem alteration. As is known for other plant diseases caused by *Phytophthora* species, the present findings confirm that management of diseases caused by *P. cinnamomi* in wild or crop lands may be difficult, because there are several variables that are not well understood which determine host infection. These include basic knowledge required for development of appropriate disease management strategies.

Several questions should be addressed to provide increased understanding of the biology and epidemiology of *P. cinnamomi* in the Americas. These include:

- Is there host specificity within individuals in *P. cinnamomi* populations?
- Which are the main determinants of host infection that may help explain the wide host range of this pathogen?
- Are phylogenetically related plant species infected by specific genetic variants or closely related groups of *P. cinnamomi* individuals?
- Why are *P. cinnamomi* populations pathogenic under highly variable edaphoclimatic and biological conditions?
- What is the genetic variability and population structure of *P. cinnamomi* populations in different hosts from the Americas?
- What role, if any, may different hosts play in pathogen survival and crop epidemics?
- Do the present analyses suggest that more available, still not exploited niches for *P. cinnamomi*?

As the area planted with avocado in Colombia is rapidly increasing, it is important to know the susceptibility of genotypes and places where there are increased probabilities of disease development, to avoid large losses in crop establishment and maintenance, and to protect natural ecosystems from the potentially severe disease caused by *P. cinnamomi*. Further research is needed to provide answer to these questions, providing knowledge that is required for establishment of effective disease management programmes.

Risk visualization of Phytophthora cinnamomi *in avocado in the Americas*

A tool to visualize the risk of *P. cinnamomi* in the Americas has been generated for its main avocado host. The risks from this pathogen are closely associated with the presence of this host. Likewise, it has been found that under certain restricted environmental requirements for the pathogen the intensity of root rot could be reduced. The models possibly under- or over-estimate the risks of *P. cinnamomi* in the many areas of the Americas, associated sampling and presence bias (Broennimann *et al.*, 2012). This is especially when this pathogen has a very broad host range (Hardham and Blackman, 2018), which has been little sampled on these two continents. Additionally, some areas classified as potential risk (south and north of the Americas), may indicate areas with unsuitable conditions for avocado. However, under climate change scenarios, these areas will present suitable conditions for the development of this host (Ramírez-Gil *et al.*, 2019).

CONCLUSIONS

Niche distribution of *P. cinnamomi* is greatly influenced by host niches. *Phytophthora cinnamomi* represented a high risk in planted and native areas with the presence of susceptible hosts throughout the Americas. This study also advances understanding of the potential distribution of the invasive pathogen *P. cinnamomi* across of the Americas.

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DATA AVAILABILITY STATEMENT

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

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