Journal of Plant Protection Research ISSN 1427-4345

ORIGINAL ARTICLE

Current and potential distributions of the most important diseases affecting Hass avocado in Antioquia Colombia

Joaquín Guillermo Ramírez-Gil[1,2]*, Andrew Townsend Peterson[2]

[1] Facultad de Ciencias Agrarias, Departamento de Agronomia, Universidad Nacional de Colombia, sede Bogota, Colombia

[2] Biodiversity Institute, The University of Kansas, Kansas, United States

Vol. 59, No. 2: 214–228, 2019

DOI: 10.24425/jppr.2019.129288

Received: November 18, 2018
Accepted: June 13, 2019

*Corresponding address:
jgramireg@unal.edu.co

Abstract

Hass avocado cultivation in Colombia has grown rapidly in area in recent years. It is being planted in marginal areas, which leads to low yields, and in many cases is related to diseases. Ecological niche modeling (ENM) can offer a view of the potential geographic and environmental distribution of diseases, and thus identify areas with suitable or unsuitable conditions for their development. The aim of the study was to assess current and potential distribution of the major diseases on Hass avocado in Colombia. Areas planted with Hass avocado in Antioquia, Colombia were sampled for diseases including the following pathogens: *Phytophthora cinnamomi, Verticillium* sp., *Lasiodiplodia theobromae*, *Phytophthora palmivora*, *Colletotrichum gloeosporioides sensu lato*, *Pestalotia* sp., and *Capnodium* sp., and one disorder hypoxia-anoxia. These pathogens were selected based on their relevance (incidence-severity) and capacity to cause damage in different tissues of avocado plants. Severity and incidence of each disease were related to environmental information from vegetation indices and topographic variables using maximum entropy modeling approaches (MaxEnt). Models were calibrated only across areas sampled, and then transferred more broadly to areas currently planted, and to potential zones for planting. Combinations of best performance and low omission rates were the basis for model selection. Results show that Hass avocado has been planted in areas highly conducive for many pathogens, particularly for *Phytophthora cinnamomi* and hypoxia-anoxia disorder. Ecological niche modeling approaches offer an alternative toolset for planning and making assessments that can be incorporated into disease management plans.

Keywords: avocado pathogens, ecological niche models, hypoxia-anoxia, risk analysis

Introduction

Avocado (*Persea americana* Mill) is cultivated in subtropical and tropical regions, particularly in the Americas, where Mexico is the top producer, with 34.5% of global avocado production (FAO 2019). Colombia is one of the countries where the area planted in avocado has increased the most in recent years. Hass avocado is the variety with the greatest cultivated area in the country (Ministerio de Agricultura y Desarrollo Rural de Colombia 2018; Ramírez-Gil *et al.* 2018). Actually, Colombia is third in the world in area planted with 35,114 ha, and Antioquia Department has the largest planted area. Colombia exported US $35 million in 2016 of which 52.7% was from Antioquia Department (Ministerio de Agricultura y Desarrollo Rural de Colombia 2018).

The rapid expansion of the area planted has led to planting in marginal areas with environmental conditions inadequate for the development of avocado plants, and the lowest use of production technologies, which has affected Colombia avocado productivity (Ramírez-Gil *et al.* 2017; Ramírez-Gil *et al.* 2018). The most notable limitations have been of a phytosanitary nature, with pathologies and disorders which are established quickly in the planted areas. These are primarily dispersed by seedlings produced in nurseries (Ramírez-Gil *et al.* 2014, 2017; Ramírez-Gil 2018).

The avocado wilt complex is considered to be the most limiting disease of this crop, affecting both roots and stems. This disease is associated with several pathogens, of which *Phytophthora cinnamomi* Rands is considered to be the most important (Zentmyer 1980, 1984; Ramírez-Gil *et al.* 2014, 2017; Hardham and Blackman 2018; Ramírez-Gil 2018). However, other causal agents, such as *Verticillium* sp., other *Phytophthora* spp., and an abiotic hypoxia-anoxia condition, can induce similar symptoms in roots and stems (Zentmyer 1984; Ramírez-Gil *et al.* 2014). Hypoxia-anoxia is an abiotic disorder associated with soil moisture, which reduces the gas content in the porous space in soil volume, especially oxygen. Avocado is susceptible to low levels of oxygen which can induce root rot. At the same time it favors pathogens such as *P. cinnamomi* infection (Stolzy *et al.* 1967; Ramírez-Gil *et al.* 2014; Sanclemente *et al.* 2014).

Other microorganisms can also produce distinct diseases in stems, leaves, fruits, and flowers of avocado, and their relevance and economic importance depend on variety, location, and type of production system. Thus, pathogens such as *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl. (= *Botryodiplodia theobromae*), *Phytophthora palmivora* (E.J. Butler) E.J. Butler, *Colletotrichum gloeosporioides* (Penz.) Penz. & Sacc. [Teleomorph = *Glomerella cingulata* (Stoneman) Spauld. & H. Schrenk], *Capnodium* sp. and *Pestalotia* sp. are also be important, because they can affect and induce disease in different avocado organs (Menge and Ploetz 2003; APS 2017).

An effective strategy in managing plant diseases is to identify areas appropriate for development of the target plant but in which environmental conditions are not favorable for the causal agents involved. Disease strategies to reduce risk such as not planting avocado in these areas need to be implemented (Agrios 2005). Ecological niche modeling (ENM) represents a powerful tool for characterizing current and potential environmental and geographic distribution of species (Peterson *et al.* 2004; Peterson 2006), based on associations between known geographic occurrences of species and environmental variation across landscapes (Peterson *et al.* 2011). Many algorithms are used in ENM, but the most popular is MaxEnt (Elith *et al.* 2011). MaxEnt is an algorithm that models the geographical distribution of a species, using presence-only data and their associated environmental variables. It is based on a general-purpose machine learning method (Phillips *et al.* 2006; Elith *et al.* 2011). MaxEnt can model projections over different spaces or periods (i.e. past, present and future) (Elith *et al.* 2011; Merow *et al.* 2013).

Ecological niche modeling has been applied to human disease systems to provide information about their ecology, distribution, risk areas of potential invasion, responses to changing climates, and identities of unknown vectors or hosts (Peterson 2006; Neerinckx *et al.* 2010; Gurgel-Gonçalves *et al.* 2012). In botanical epidemiology, ENM approaches have not been widely used. A few studies have used ENM to investigate potential geographic distributions of plant diseases (Kluza *et al.* 2007; Galdino *et al.* 2016; Burgess *et al.* 2017; Narouei-Khandan *et al.* 2017). In the study were used ENM approaches to evaluate current and potential distributions of the most important pathogens and disorders of Hass avocado in Antioquia, Colombia.

Materials and Methods

Occurrence data

In the study were used data associated with the incidence and severity of seven pathogens and one disorder present in Hass avocado production fields in Antioquia Department, Colombia to model their current and potential distribution. The study areas, divided into northern, eastern, and southwestern sectors, had an elevation between 1,800 and 2,500 m, corresponding to lower tropical montane humid forest. The trees sampled were all Hass variety grafted onto West Indian rootstock, at planting distances of 5 × 6 m; 5 × 7 m; 6 × 6 m and 6 × 7 m as reported elsewhere (Ramírez-Gil *et al.* 2017). The evaluation of incidence and severity was based on equations 1 and 2 in 46 commercial plots over three time periods (2011–2012, 2013–2014, and 2015–2016) with two evaluations per year, one in the dry season (December-January) and the other in the rainy season (April-May). All the plots were evaluated according to a proportional stratified (number of plots planted in each region of Antioquia) sampling. In each lot, the number of plants to be sampled was obtained by simple random sampling, using the maximum variance formula (Cochran 1977). In each plot, geographic coordinates were recorded using a Triple Series GeoXT GPS system set to UTM Zone 18 N (based on WGS 84 projection). The geographical location is reported in Figure 1.

Pathogens were diagnosed via a polyphasic approach. Suitable symptomatic descriptions were included, supplemented by laboratory analysis with isolation protocols as described by Ramírez-Gil *et al.* (2014). Morphological identifications were based on taxonomic codes for fungi genotypes reported by Barnett and Hunter (1972), and Seifert *et al.* (2011), and Erwin and Ribeiro (1996) for *Phytophthora* species. Abiotic factors were identified according to the apparent source or causality associated with specific

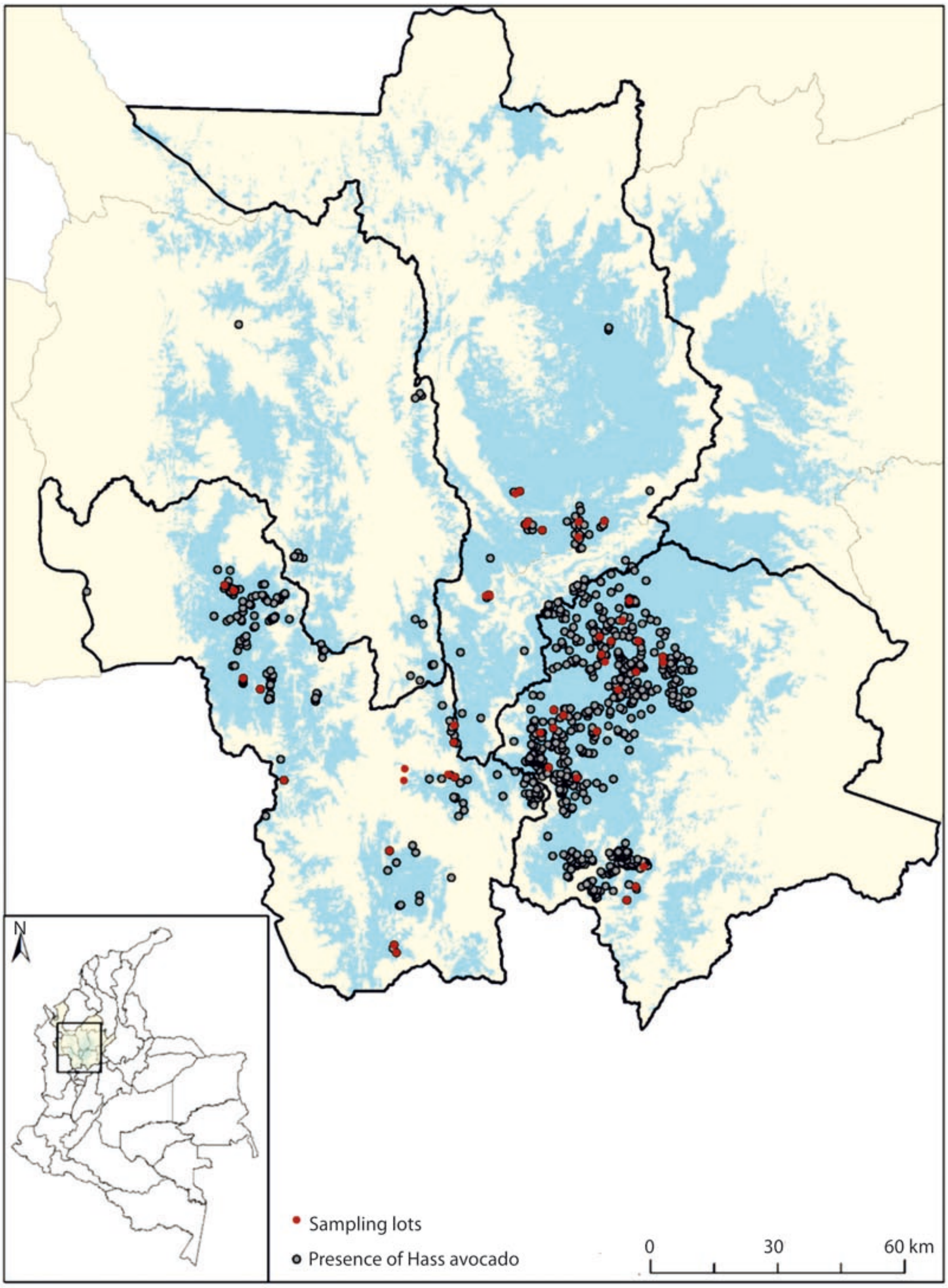

Fig. 1. The Hass avocado growing area and region studied for modeling of diseases and disorders in Antioquia Department, Colombia

Black lines indicate the three sampling regions (northern, eastern, and southwestern), and blue-shaded areas (inside area) are actual and potential areas for this crop (Ramírez-Gil *et al*. 2018), used as transfer regions for ecological niche models. Red circles (filled) indicate lot samples for disease occurrence. Gray circles (without filled) indicate lots of avocado

disorders. For each causal agent, the respective pathogenicity test was carried out (all parameters can be seen in Table 1). Those resulting positive for biotic agents were subjected to molecular confirmation for sequencing the internal transcribed spacer (ITS) regions using polymerase chain reaction (PCR) based on the primer pairs ITS5-ITS4 and ITS1-ITS4 (White *et al.* 1990). PCR products were purified and sequenced using the Macrogen service. Sequences were edited using the software Bioedit and compared to databases at NCBI using the algorithm Blastn implemented in the web page (http://www.ncbi.nlm.nih.gov/BLAST/Blast.cgi, 24/10/2017).

Seven causal agents and one disorder were selected, based on their frequency and importance in the region and capacity to affect different parts of the plants. Four

Table 1. Pathogenicity tests of pathogens in avocado – supporting information Table 2

Causal agent	Tissue isolated	Incubation period				Re-isolated
		a	b	c	d	
Phytophthora cinnamomi	roots	17.6	na	na	na	+
Verticulllium sp.	roots	27.8	na	na	na	+
Hipoxia-anoxia	na	38.4	na	na	na	na
Phytophthora palmivora	roots and leaves	25.3	na	29.3	na	+
Lasiodiplodia theobromae	roots, stems, leaves	19.3	23.2	47.4	na	+
Pestalotia sp.	leaves and fruits	na	na	35.2	42.3	+
Colletotrichum gloeosporoides sensu lato	stems, leaves, and fruits	na	42.3	21.2	−15.3	+
Capnodium sp.	stems, leaves, and fruits	na	45.3	33.4	48.4	na

a – inoculation in roots, b – inoculation in the stems, c – inoculation in leaves, d – inoculation in fruits; na – not applied. Pathogenicity tests were made based on the method reported by Ramírez-Gil *et al.* (2017), and Ramírez-Gil *et al.* (2014), using healthy avocado seeds and seedlings from Hass variety, growing in sterile substrate. When plants had five fully expanded leaves and a well-developed secondary root system, isolated microorganisms were inoculated on the same organs of avocado plants from which they were isolated (i.e. seed, roots, stems, and leaves). For microorganisms isolated from roots, 200 ml of inocula solution (PDA-SDW) at a concentration of 1×10^3–1×10^6 infective propagules per ml^{-1} were added in four equidistant parts in substrate. A similar solution (200 ml of inocula at 1×10^3 infective propagules ml^{-1}) plus 2 g · l^{-1} of agar (Difco, USA) for adhesion improvement, was prepared for inoculation of microorganisms isolated from seeds, stems, and leaves, and was sprayed over the surface of corresponding tissue. In addition, all microorganism that were positive were re-isolated. For hypoxia-anoxia conditions in roots, the guidelines reported by Ramírez-Gil *et al.* (2014) were followed, planting seedlings in pots with a moisture regime in soil greater than 70%

causal agents and one disorder were associated with the avocado wilt complex (each causing specific symptoms), and these included *P. cinnamomi*, *Verticillium* sp., *L. theobromae,* and *P. palmivora*, as well as the disorder of abiotic origin in the case of hypoxia-anoxia. The other three pathogens were associated with pathologies in leaves, stems, and fruits. *Colletotrichum gloeosporioides sensu lato, Pestalotia* sp., and *Capnodium* sp. *P. palmivora,* and *L. theobromae* were selected, which were associated with the avocado wilt complex, as well as provoking symptoms in stems, leaves, and fruits. *Colletotrichum gloeosporioides sensu lato* affects seeds, stems and fruits, whereas *Pestalotia* sp. and *Capnodium* sp., affect leaves and fruits.

For *P. cinnamomi* and hypoxia-anoxia, which were nearly ubiquitous across all sampling sites, were used the intensity of the disease (severity), quantified as the area under the disease progress curve (*AUDPC*) (Madden *et al.* 2017) (equation 1). Intensities were used as the basis for occurrence data. This measure is based on a specific scale for these pathologies developed in the work group, since incidence is not a good measure for these tow causal agents (Ramírez-Gil *et al.* 2017). For the remaining pathologies, incidence was used with occurrence data calculated as the percentage of total plants that were infected (equation 2).

$$AUDPC = \sum_{i=1}^{n-1} \frac{y_i + y_{i+1}}{2} x(t_{i+1} - t_i), \qquad (1)$$

where: AUDPC – area under the disease progress curve, y_i – assessment of a disease (ordinal score) at the i-th measures, t_i – time (month) at the i-th measures, n – the total measures.

$$I = \frac{DP}{TP} \times 100\,[\%], \qquad (2)$$

where: *I* – incidence, *DP* – diseased plants, *TP* – total plants.

Environmental variables

The environmental variables were derived from fine-resolution satellite imagery, specifically based on the normalized difference vegetation index *(NDVI)*, in the form of 16-day composite images (2009–2016) with a spatial resolution of 250 m, from the Moderate Resolution Imaging Spectroradiometer (MODIS) sensor (http://reverb.echo.nasa.gov). The *NDVI* is the most common vegetation index used in ecological niche modelling to determine the current and potential disease distribution (Peterson 2014). MODIS data were downloaded and reprojected using the MODIS Reprojection Tool (MRT) (https://lpdaac.usgs.gov/tools/modis_reprojection_tool_swath). Because MODIS data often include data gaps caused by cloud cover, we filled these gaps via a spatial and temporal interpolation process implemented for this study by Huijie Qiao (Chinese Academy of Sciences). Other environmental variables were obtained from the GMTED (Global Multi-resolution Terrain Elevation Data) Digital Elevation Model (DEM), with spatial resolution of 230 m (https://topotools.cr.usgs.gov/GMTED_viewer/). From the DEM, data layers summarizing elevation (*E*), slope in degree (*SD*), slope in percent (*SP*), terrain ruggedness index (*TRI*), and topographic position index (*TPI*), using the raster package in R (R Core Development Team 2017) were derived.

Here, to reduce the dimensionality of the data (Peterson 2007; Peterson and Nakazawa 2008; Varela *et al.* 2014; Ramírez-Gil *et al.* 2018), given the large number of NDV images used in this work (more than 400), was applied principal components analysis (PCA) using Spatial Analysis Tools in ArcGIS (version 10.5). This process generated 128 components. The first 20 (1–20) components were retained, which together explained 54% of the total variance for analysis. Correlations among variables (NDV and topographies) was assessed using R (R Development Core Team 2017), eliminating one from each pair of variables presenting Pearson correlation coefficients ≥0.8. Based on this, *TRI* and *SP* from analysis were removed.

Ecological niche modeling (ENM) and evaluation

The niche modeling process must start with a correct definition of the calibration area (M), which is equivalent to the accessible area of species (Barve *et al*. 2011; Saupe *et al*. 2012). The study was focused on sampled areas (northern, eastern, and southwestern) for diagnosis of pathogens and disorders in avocado crops across Antioquia Department (Fig. 1). Given that the Hass avocado production system is growing rapidly in the region (Ministerio de Agricultura y Desarrollo Rural de Colombia 2018), models were transferred more broadly across all areas where this crop is currently planted or conditions are suitable for planting (Ramírez-Gil *et al*. 2018) (Fig. 1). Selection of environmental variables is another important step. Twenty three variables (PCA 1-20 obtained from *NDVI*, *TRI*, *E*, and *SD*) were set, and the jackknife test with logistic output format routines in Maxent (version 3.3.3k) (Phillips *et al*. 2006) was used to identify and eliminate layers showing low contribution to model predictions. This process was done iteratively, removing 1–2 variables per step; variables used in each model are reported in Table 2. In addition, different combinations of regularization coefficients (0.1, 0.3, 0.5, 1, 1.5, 2, 3, 4, 5, and 10) and feature combination linear (L), quadratic (Q), product (P), threshold (T) and hinge (H) (L, LQ, LQP, LQPT, and LQPTH) in Maxent algorithm were tested. The best model was tested based on Akaike Information Criterion (AIC_c) values calculated in ENMTools (version 1.3) (Warren *et al*. 2010) from models calibrated with 100% of input points, 10 cross-validated replicates, and raw model outputs in Maxent (Phillips *et al*. 2006) (Table 2).

Because *P. cinnamomi* and hypoxia-anoxia were ubiquitous, and because severity values are important for these two diseases, Neerinckx *et al*. (2010) concepts were followed. In basing binary presence data on different cut-off thresholds ENMs were developed based on different subsets of occurrence points, from high-severity "high" to medium-to-high severity "middle" and any degree of severity "any". Values in each range are given in Table 2. In each case, the data above the threshold were divided five times randomly into equal halves for model calibration and evaluation (see below). For the remaining diseases, incidence was divided into two subsets of occurrence points: (i) high-incidence "high" and (ii) any incidence "any"; incidence values for each species used as cut are presented in Table 2. ENMs were developed using Maxent (version 3.3.3k) (Phillips *et al*. 2006), with 10 bootstrap replicates, logistic output format, and settings (Table 2).

For *P. cinnamomi* and hypoxia-anoxia, ENM prediction was evaluated using partial receiver operating characteristic (partial ROC) approaches (Peterson *et al*. 2008), via functions available in Niche Toolbox (http://shiny.conabio.gob.mx:3838/nichetoolb2/). An acceptable omission rate of *E* = 5% and ran 1000 replicate analyses were used based on random subsamples of 50% of the evaluation data. The probability was associated with the test as the proportion of replicate analysis in which the partial ROC statistic was ≤1. To evaluate performance, the omission rate (*OR*) via thresholding model predictions on the calibration data was calculated, based on the highest model output value associated with 5% omission of calibration data. This threshold was applied to the models and *OR* was calculated based on the independent evaluation data. The *OR* is defined as the maximum tolerable amount of errors within a model, in this case confirmed presences, which are omitted by the model by simple statistical probability.

For *Verticillium* sp., *P. palmivora*, *L. theobromae*, *C. gloeosporioides sensu lato, Pestalotia* sp., and *Capnodium* sp., for which sample sizes were smaller, significance was evaluated based on a jackknife test, using software given in supplementary information (Pearson *et al*. 2007). All possible combinations of points were made, in which each point was removed one time from the set of occurrence points, and a model was built using the remaining $n - 1$ occurrences; models were calibrated using 100% (n) of input points. In this case an index of *OR* was calculated as the proportion of cases in which the model replicate was viable to predict the single occurrence excluded from model training.

Based on significance, complexity, and performance for the ENMs generated, the best models (Table 2) were selected, and transferred across the areas planted in or with potential for cultivation of Hass avocados in Antioquia Department (Ramírez-Gil *et al*. 2018) (Fig. 1). Maxent was used, with 100% of calibration points for training, 10 bootstrap replicates, no clamping or extrapolation, logistic output format, and settings reported in Table 2. Suitability values for each plot sampled for disease presence were extracted using Spatial Analysis Tools in ArcGIS 10.3. Incidence and severity in each plot with the technological level (TL)

Table 2. Parameters of niche models for the eight most important diseases in Hass avocado lots across Antioquia Department, Colombia

Disease	Severity or incidence	Range of severity[a] and incidence [%]	Environment variables	Regularization multiplier	Features	*p* value	*OR* [%]	Area predicted [%]
Phythophthora cinnamomi[1]	high	>40.30	PCA 4, 5, 6, 7, 11, 13, 16 and *SD*	2	LQ	$p < 0.001$[b]	14.80	64.4
	middle	30.00–40.29	PCA 4, 5, 6, 7, 10, 13, 16 and *SD*	2	LQ	$p < 0.001$[b]	9.70	78.6
	any	<29.90	PCA 4, 5, 6, 7, 11, 13, 16 and *SD*	3	LQ	$p < 0.001$[b]	4.50	85.3
Hypoxia-anoxia[1]	high	>27.20	PCA 6, 7, 9, 10, 13, 16, 19, 20 and *SD*	1.5	LQP	$p < 0.001$[b]	10.30	33.8
	middle	27.10–17.60	PCA 6, 7, 9, 10, 13, 16, 19, 20 and *SD*	1	LQ	$p < 0.001$[b]	15.30	25.4
	any	<17.50	PCA 6, 7, 9, 10, 13, 16, 19, 20 and *SD*	1	LQP	$p < 0.001$[b]	17.70	18.5
Lasiodiplodia theobromae[2]	high	>2.00	PCA 1, 5, 8, 13, 17, 18, 19 and *E*	3	LQP	0.011807[c]	20.00	28.61
	any	<1.99	PCA 1, 5, 8, 13, 17, 18, 19 and *E*	3	LQ	0.009995[c]	18.10	43.83
Phythohthora palmivora[2]	high	>1.60	PCA 1, 4, 5, 13, 14 and *E*	4	LQ	0.000136[c]	50.00	2.06
	any	<1.59	PCA 1, 4, 5, 13, 14 and *E*	2	LQ	0.000551[c]	8.34	43.73
Verticillium sp.[2]	high	>2.50	PCA 3, 10, 12, 13, 14 and *SD*	2	LQP	0.076286[c]	33.34	31.15
	any	<2.49	PCA 3, 10, 12, 13, 14 and *SD*	2	LQ	0.002404[c]	25.00	32.4
Colletotrichum gloeosporioides[2]	high	>1.45	PCA 4, 6, 10, 11, 12, 13, 14 and *E*	3	LQP	0.014722[c]	33.34	20.0
	any	<1.44	PCA 4, 6, 10, 11, 12, 13, 14 and *E*	1.5	LQ	0.018274[c]	28.40	34.0
Pestalotia sp.[2]	high	>9.50	PCA 1, 4, 5, 11, 13, 17, 19, 20 and *E*	1.5	LQ	0.000300[c]	30.10	7.33
	any	<9.49	PCA 1, 4, 5, 11, 13, 17, 19, 20 and *E*	2	LQ	0.000173[c]	20.15	48.78
Capnodium sp.[2]	high	>1.3	PCA 1, 4, 5, 7, 8, 12 and *E*	2	LQ	0.003859[c]	16.67	27.4
	any	<1.29	PCA 1, 4, 5, 7, 8, 12 and *E*	3	LQP	0.020085[c]	12.50	41.72

[1]values of severity; [2]values of incidence; [a]area under the disease progress curve (*AUDPC*); [b]partial-ROC; [c]jackknife test; high, medium, any – categories associated with levels of infections and incidence of pathologies; PCA – principal components analysis from *NDVI*; *SD* – slope of terrain in degree; *E* – elevation (m); feature combination linear (L), quadratic (LQ), product (LQP); *OR* – omission rate

of the plot were associated. The TL was classified as low, medium, or high in a previous analysis (Ramírez-Gil *et al*. 2017). The concept (TL) is associated with a series of agronomic and management practices in avocado plots, which have been related through statistical and mathematical relationships with different levels of incidence, severity, and mortality in avocado plots (Ramírez-Gil *et al*. 2017).

Results

Model selection and evaluation

The dimensionality and number of environmental variables were reduced when the principal components analysis of the *NDVI* layers showed a gradual accumulation of total variance. For practical reasons and computer performance the study was focused on the first 20 components derived from NDVI, which explained 54% of the overall variance. Based on correlation analysis, the topographic dimensions to just E, SD, and TPI, which were relatively uncorrelated ($r \leq 0.80$), were reduced.

Jackknife analyses in Maxent, led to identify and retain between 6 (*P. palmivora, Verticillium* sp.), 7 (*Capnodium* sp.), 8 (*L. theobromae, C. gloeosporioides*), and 9 (*P. cinnamomi*, hypoxia-anoxia, *Pestalotia* sp.) environmental variables (Table 2) for modeling. Furthermore, based on variation of parameters of Maxent, the best model was associated with regularization multiplier between 1 and 4, and features LQ and LQP. The process previously described improved the capacity of prediction of the models, increasing statistical significance ($p < 0.01$), high performance based on low omission (*OR*) values, and lowest complexity (low AIC) (Table 2).

All combinations of the severity levels for *P. cinnamomi* and hypoxia-anoxia yielded ENM predictions that performed better than random ($p < 0.001$) in partial ROC tests. For *P. cinnamomi* the ENM with the lowest *OR* (4.5%) was that based on all severity levels; models based on high-severity lots only had the highest *OR*s (14.8%). However, hypoxia-anoxia was quite distinct with the lowest *OR* (10.30%), which was obtained when models were based on highest severity lots only. Models based on any level of severity had the highest *OR* (17.7%) (Table 2).

For the remaining pathologies evaluated, the Pearson small sample jackknife test indicated that all predictions (high and low incidence) were statistically better than random ($p < 0.001$). In all cases, the *OR* was higher when models were based on high-incidence sites. This effect was particularly evident for *P. palmivora* and *Pestalotia* sp., with *OR* of 50.0% and 30.1 %, versus 8.34 and 20.2% respectively (Table 2).

Based on the transfer of the models developed to the current cultivated regions and with potential to be planted in the future, the most informative models for *P. cinnamomi* were those in which sites with any severity levels were used. For hypoxia-anoxia, highest-severity sites only were used; and for all other pathologies, any-incidence sites in the calibration of final models were used.

Current and potential distributions of pathologies

The known distribution of *P. cinnamomi* and the most suitable areas for this pathogen coincided with the extent of production in areas in Antioquia Department, particularly in the eastern regions, the area of highest production. Its potential distribution coincided with the highest-suitability areas for avocadoes. The area identified as suitable for this pathogen was broadest when based on any severity (85.3% of areas currently planted and with environmental potential to be planted in Antioquia Department), followed by medium severity (78.6%). Finally, the smallest area was identified by models based only on high-severity points (64.4 %) (Fig. 2, Table 2).

For hypoxia-anoxia, again, results were contradictory. ENMs based on high-severity points identified the broadest area (33.8%). Models based on lower severity levels identified narrower areas (medium 25.4%; low 18.5%). Suitable areas for this pathology were concentrated on the high plateaus of the eastern and northern regions of the study area, and to a lesser degree in the southwestern regions. Areas presenting low suitability for this disease but with high suitability for avocadoes were on the upper slopes of the Río Cauca in the southwestern and western parts of Antioquia (Fig. 2).

For *Verticillium* sp., ENMs based on high and any incidence identified 31.2 and 32.4% of the study region as suitable, respectively. These suitable areas were focused on the high plateaus of the eastern and northern parts of the department (Fig. 3). For *L. theobromae,* ENMs based on high and any incidence identified 20.0 and 18.1% of the study area as suitable, respectively. The distributional potential of this pathology was focused in the southwest and on the high plateaus of eastern Antioquia (Fig. 3). For *P. palmivora,* ENMs based on high-incidence sites only were significant ($p < 0.0001$), but the suitable area identified was quite small (2.0%). For models based on any incidence, the suitable area was broader (43.7%), mostly in the high plateaus of eastern and southwestern Antioquia (Fig. 3).

For *Pestalotia* sp., ENMs based on high and any incidence points identified 7.3 and 48.8% of the study area as suitable, respectively. Suitable areas for this pathology were concentrated in southwestern and eastern Antioquia (Fig. 4). For *C. gloeosporioides sensu lato*, the high-incidence model identified 20.0% of the region as suitable, particularly in northern Antioquia. ENMs based on any occurrences had a broader suitable area (34.0%), distributed more evenly across the region (Fig. 4). For *Capnodium* sp., suitable areas covered 27.4 and 41.7%, of the region for high and any incidence data, respectively. Much of the avocado production area in Antioquia appears suitable for this pathology, particularly in the eastern parts of the department (Fig. 4).

Areas presenting suitable conditions for the presence of the eight most important pathologies of Hass avocadoes in the study region (Figs. 2, 3, 4; Table 2) were associated closely with areas currently planted with this crop as well as areas which are expected to be planted in avocado in coming years. This situation implies that the distribution predicted for the pathogens in these areas could be considered as potential, since

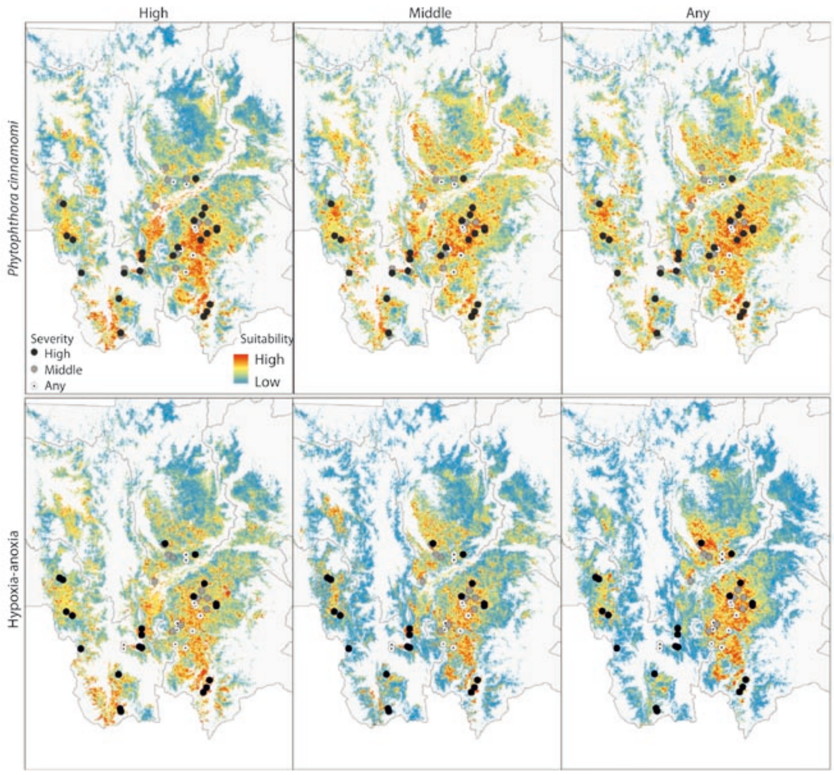

Fig. 2. Projection of potential distribution of *Phytophthora cinnamomi* and hypoxia-anoxia diseases and disorders in Hass avocado in Antioquia Department, Colombia

Dots represent: high (black), middle (gray), and any (white with black center) are three levels of infection and severity used as criteria for establishing the presence of *Phytophthora cinnamomi* and hypoxia-anoxia

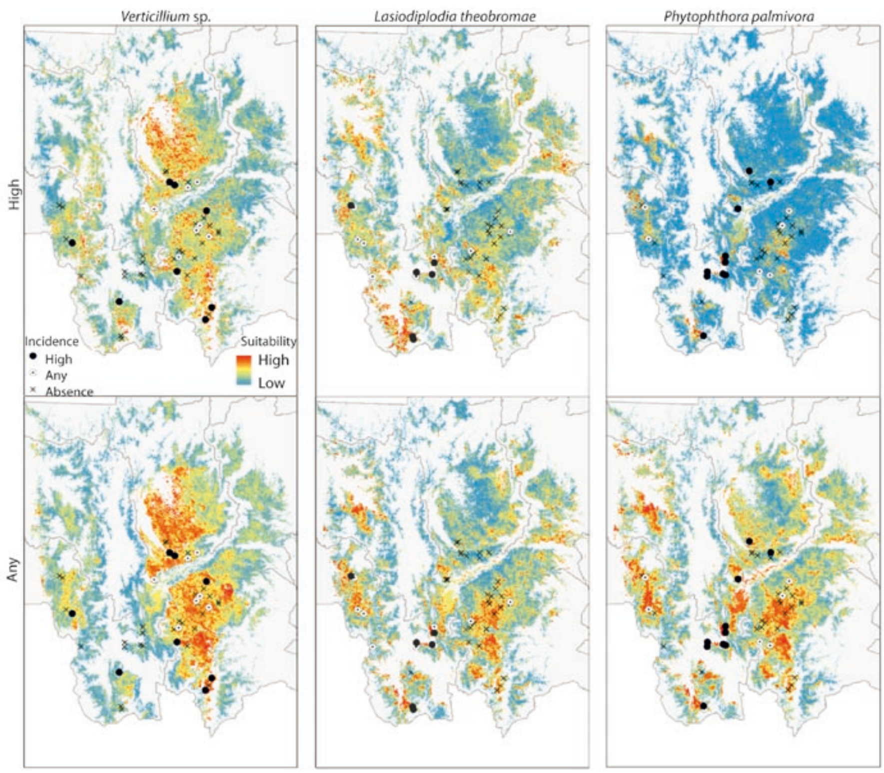

Fig. 3. Projection of potential distribution of *Verticillium* sp. *Lasiodiplodia theobromae*, and *Phytophthora palmivora* in Hass avocado in Antioquia Department, Colombia

Dots represent: high (black), any (white with black center) and absence (x) are two levels of incidence and absence used as criteria for establishing the presence of *Verticillium* sp., *Lasiodiplodia theobromae*, and *Phytophthora palmivora*

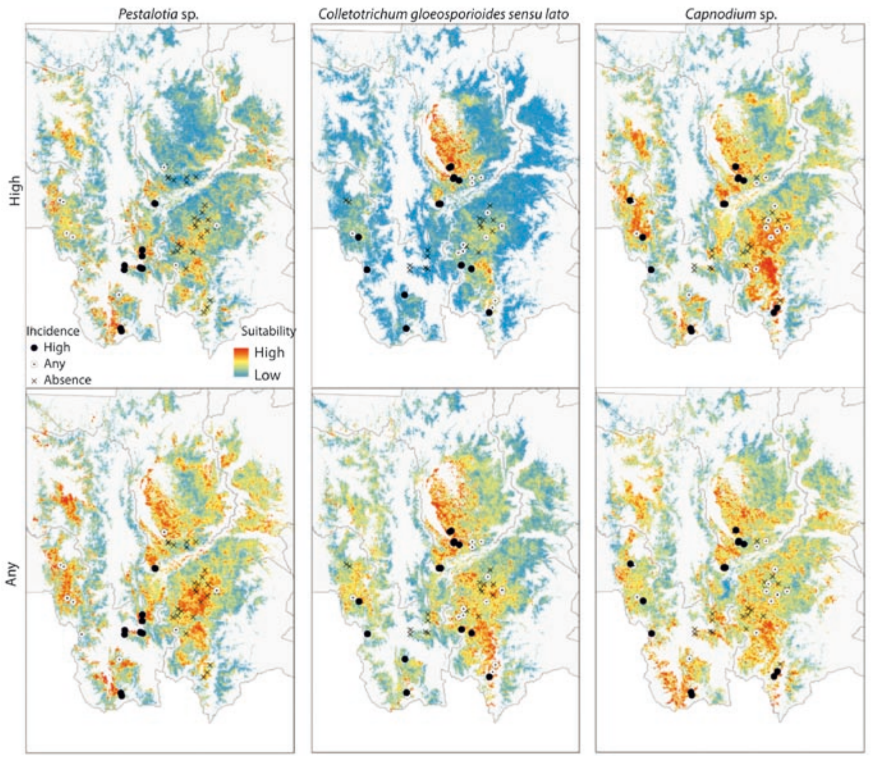

Fig. 4. Projection of potential distribution of *Pestalotia* sp., *Colletotrichum gloeosporioides sensu lato* and *Capnodium* sp. in Hass avocado in Antioquia Department, Colombia

Dots represent: high (black), any (white with black center) and absences (x) are three levels of incidence used as criteria for establishing the presence of *Pestalotia* sp., *Colletotrichum gloeosporioides sensu lato* and *Capnodium* sp.

the host is not currently present, but there are environmental conditions for the disease to develop.

Relationship of avocado production plots to disease-suitable areas

The majority of the plantations sampled in this study were above the average omission thresholds in each of the niche models based on different severity levels (high, medium, any) for *P. cinnamomi* and for hypoxia-anoxia, as well as for incidence (high, any) for *L. theobromae*, *P. palmivora*, *Verticillium* sp., *C. gloeosporioides sensu lato, Pestalotia* sp., and *Capnodium* sp. (Figs. 5, 6). For *L. theobromae*, *P. palmivora*, *Verticillium* sp., *C. gloeosporioides sensu lato, Pestalotia* sp., and *Capnodium* sp., absence of the disease did not group at any particular probability value in the niche models; rather, they were quite dispersed at different values (Fig. 6).

As regards the assessment of numbers of pixels according to the different niche models generated in this study, was found that areas presently planted and found to be suitable for planting avocado in the study region show similar proportions of areas at low and medium-high suitability for development of *P. cinnamomi* at high severity, but for incidence medium or any, most were at an intermediate level of suitability (Fig. 5). For hypoxia-anoxia, niche models based on medium and any severity, most pixels in the study region were at low suitability values, whereas the niche model based on high severity showed a more uniform distribution of favorability (Fig. 5).

As regards the number of pixels associated with favorability for the other pathologies, some contrasts were noted. For *Verticillium* sp., *L. theobromae, Pestalotia* sp., and *Capnodium* sp., niche models based on high or any incidence the numbers of pixels diminished with the suitability for the disease, whereas for *P. palmivora*, the niche model for high incidence had the majority of pixels at low suitability, and the niche model at any incidence had a more uniform distribution of probabilities. For *C. gloeosporioides sensu lato*, the niche model based on high incidence showed few high-suitability pixels, whereas based on any incidence there was a more uniform distribution (Fig. 6).

Discussion

Selection and evaluation of models

In recent years there has been an increase in the use of ENMs approach, given its multiple applications. This situation has generated the massive use of these tools,

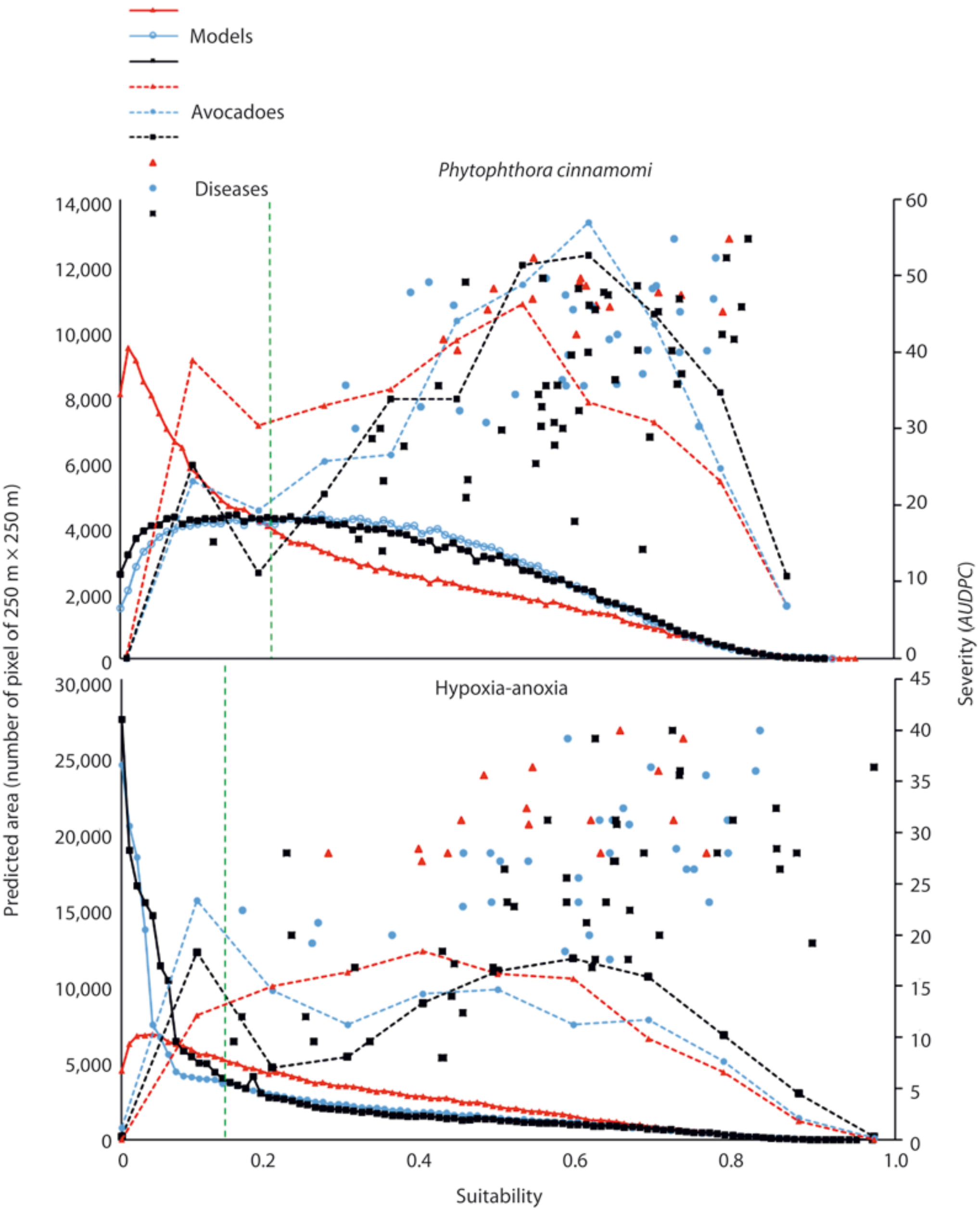

Fig. 5. Area associated with suitability for the presence of *Phytophthora cinnamomi* and hypoxia-anoxia and presence of plots planted with avocado based on ecological niche models in Antioquia Department, Colombia

▲ – high severity, ● – middle severity, ■ – any severity. Vertical line shows average of omission rate of 5% for ENMs (high, middle, and any incidence). Dots represent the severity in plots sampled. Broken lines represent the number of pixel (area) when the plots were planted under different suitability for the presence of *Phytophthora cinnamomi* and hypoxia-anoxia; *AUDPC* – area under the disease progress curve

with the problems that this implies, given the low predictive capacity of some models (Peterson *et a*l. 2011). That is why in this work, with the objective of better predicting the ENM, algorithms for its calculation, different strategies were applied: 1 – define an appropriate M, which is based on the knowledge of the species to be modeled (Barve *et al.* 2011; Saupe *et al.* 2012), 2 – reduce the dimensional and number of the environmental variables, eliminating those with lower capacity of prediction (Peterson 2007; Peterson and Nakazawa 2008; Varela *et al.* 2014), and explore the different parameters of the algorithm Maxent (i.e. regularization multiplier and features) (Merow *et al.* 2013; Ramírez-Gil *et al.* 2018)

Correct selection of environmental variables is a fundamental step in developing ENMs, which are based on environmental characteristics of areas of known occurrence and of sites where the species is not known to be present (Phillips *et al.* 2006). For the development of pathologies in plants, different environmental dimensions determine specific conditions that favor (or not) expression of particular diseases (Agrios 2005). In the study was found that the first principal components (1–20) extracted from the *NDVI* values

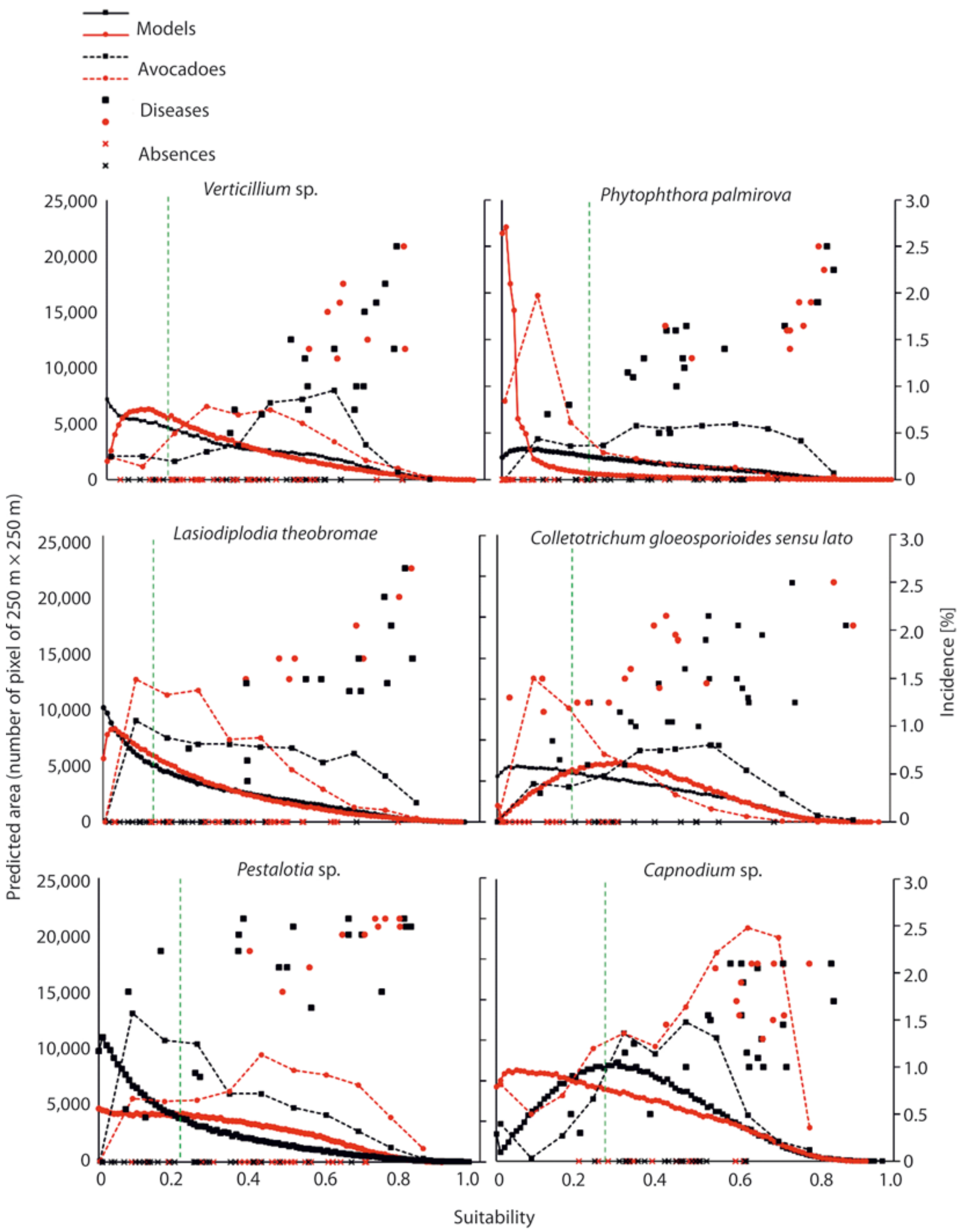

Fig. 6. Area (number of pixels) associated with suitability for the presence of *Verticillium* sp., *Lasiodiplodia theobromae*, *Phytophthora palmivora*, *Pestalotia* sp., *Colletotrichum gloeosporioides* and *Capnodium* sp. and the presence of plots planted with avocado based on ecological niche models in Antioquia Department, Colombia

● – high incidence, ■ – any incidence. Horizontal line shows average of omission rate of 5% for ENMs (high, middle, and any incidence). Dots represent the severity in plots sampled. Broken lines represent the number of pixel (area) when the plots were planted under different suitability for the presence of *Verticillium* sp., *Lasiodiplodia theobromae*, *Phytophthora palmivora*, *Pestalotia* sp., *Colletotrichum gloeosporioides* and *Capnodium* sp.

were particularly informative; for some of the pathologies, elevation (*E*) and slope (*SD*) were also important. Extremely important variables such as precipitation, anthropomorphism, soil properties, among others in plant pathologies and disorders were not evaluated in this work, because they are very complex and expensive to determine, especially to a fine resolution. In addition, these variables can be determined indirectly through *NDVI* and topographic variables (Huete *et al.* 2002; Malhi *et al.* 2010; Pettorelli 2013).

The *NDVI*-based variables have high spatial resolution (250 m) and take into account temporal dynamics at 16-day temporal resolution and are available for all periods up to 2000 (Table 2). *NDVI* summarizes the types and mass of vegetation across landscapes, and can capture biophysical patterns through time and space in response to the environmental conditions (Huete *et al.* 2002; Pettorelli 2013). *NDVI* has been used to detect changes in the reflectance as a consequence of different types of stress in plants, including those generated by diseases and disorders, in which its processing implies the need to simplify the data, commonly using the PCA (Lu *et al.* 2018). In the tropics, elevation relates closely to temperature and to a lesser degree to precipitation and relative humidity (Malhi *et al.* 2010). Environmental variables are directly related with infection processes in plant pathogens (Agrios 2005). Slope, on the other hand, is associated with surface water flow, which is of considerable importance in disease dynamics in avocadoes, especially the avocado wilt complex and their causal agent studied in this work (Ramírez-Gil *et al.* 2014; Ramírez-Gil 2018).

The approach of this study was that of developing niche models based on different levels of severity or incidence of different diseases, with models calibrated on areas sampled, and transferred across areas where avocado are actually or potentially grown. These models made distributional predictions for each disease that were significantly better than random predictions, making it clear that each disease has an ecological niche that overlaps that of avocado only partially and not completely. Except for hypoxia-anoxia, niche models based on high incidence tended to make predictions that had higher associated omission rates and smaller predicted suitable areas. This outcome could be the result of 1 – a disease which reaches high severity or incidence regardless of the environmental conditions manifested at a site, or 2 – environmental conditions associated with high severity or incidence are manifested only to a very small extent that would then exclude many existing plantations.

The results of the potential distribution of the pathogens and disorder reported in this work were the result of a modeling process, where the predictive variables were *NDVI*, elevation, and slope, associated with the presence based on a sample in the study area. A pathological relationship is very complex and depends on the relationships with the host, the production system (anthropic), positive and negative symbiosis with other species associated with the agroecosystem, which are quite difficult to evaluate.

Current and potential distributions

The pathology caused by *P. cinnamomi* is presently broadly distributed, and presented models corroborated this point suggesting that this pathogen and Hass avocadoes have very similar distributional potential across Antioquia (Fig. 2). *Phytophthora cinnamomi* is considered to be the most important pathogen for this crop, and has been reported from all avocado production areas worldwide, as well as in other fruit and forestry species (Zentmyer 1980; Ramírez-Gil *et al.* 2014; Hardham and Blackman 2018). Its broad distributional potential likely relates to great adaptability to different environmental conditions. The pathogen is known to infect >3,000 host plant species (Ramírez-Gil *et al.* 2014; Hardham and Blackman 2018), and it has been considered as an invasive species (Bohlen 2006; Burgess *et al.* 2017). Presented in this study models certainly reflected these facts, as the entire Hass production system in Antioquia seems to be vulnerable to this pathogen.

The hypoxia-anoxia pathology was associated with the high plateaus in northern and eastern Antioquia. This pathology appears to have an abiotic origin associated with moisture and low oxygen in the soil matrix. This phenomenon is associated with high precipitation and low drainage capacity in the soil (Ramírez-Gil *et al.* 2014). As such, particularly at high incidences, the distribution of this pathology is more limited than the previous one, which makes it less problematic for Hass avocadoes in Colombia (Fig. 2).

For the pathologies associated with *Verticillium* sp., *L. theobromae*, *P. palmivora*, *C. gloesporiodes sensu lato, Pestalotia* sp., and *Capnodium* sp., our ENMs identified suitable areas for each with statistical significance. These results are useful to efforts aimed at sustainable management of these less-pervasive but problematic pathologies. Such results are particularly relevant in light of the scanty knowledge about them (Ramírez--Gil *et al.* 2014, 2017).

The approach in this study included determining the existing or potential distribution of the main diseases in areas where avocado is planted in Antioquia, Colombia. Models were also applied to the set of sites where this crop could be planted in the future. That is, the results are not only applicable to the areas where avocado is currently planted, but also to areas where avocado could be planted, giving an idea of potential problems with diverse pathogens that such planting efforts might encounter.

The use of ENM in botanical epidemiology is recent and not very common, and includes the results obtained in this work and in others (Kluza *et al.* 2007; Galdino *et al.* 2016; Burgess *et al.* 2017; Narouei-Khandan *et al.* 2017). The ENM tool can be integrated into the management of plant diseases in order to identify the potential areas where there is a risk of establishing specific pathogens or disorders. This information can be used to propose strategies for preventing the exclusion (not planting in areas with high suitability for pathogens), for increasing the quality of seedlings produced in nurseries, for identifying disease hosts in avocado growing areas, or for designing specific management practices based on edaphic and climatic conditions, hosts, and anthropogenic relationships.

Avocado production areas in relation to pathologies

More generally, was noted that essentially all Hass avocado production areas in Antioquia are also favorable for multiple pathogens and disorders for the crop, meaning that no area is free from the pathological problems examined in this paper. However, for all pathologies examined, except *P. cinnamomi* and hypoxia-anoxia, many production lots were not affected, even though they were predicted to have favorable conditions for the disease. This situation likely has multiple causes, e.g. specifically effective control of pathogens via different management practices (Fig. 7). Another possibility, however, is that these diseases indeed have distributional potential, but they are not present in all zones evaluated, thereby representing ongoing threats to the crop.

One important aspect of understanding the distribution of plant diseases is that they depend not only on the environmental conditions, but also on interactions that the pathogens may or may not have with their hosts, the population dynamics of the pathogen, and other aspects of agronomic practices related to the host (Agrios 2005), particularly if the plantation is part of a commercial operation. This situation explains why in many lots in the study region which were planted at high technology levels with Hass avocados there may not be many problems with diseases, in spite of high suitability for the latter. At sites with lower suitability, incidences may be higher in low-technology systems. The direct relationship between technological level and incidence is an additional factor besides environmental conditions (Fig. 7).

This study is the first to focus on Hass avocado production systems using ecological niche models to assess suitability for diseases. The seven pathogens and one disorder were assessed, that are most important for this crop in this region and analyzed each at different levels of severity or incidence, producing different high resolution (250 m) risk maps in current and potential avocado growing areas in Antioquia Colombia. This approach offers practical applications for integrated management of plant diseases relevant to avocado, which could be applied in planning future planting areas for this crop, and finding areas that would exclude the most serious diseases.

Acknowledgements

Dr Huijie Qiao assisted with removing cloud contamination from satellite imaginary. The Universidad Nacional de Colombia sede Medellín provided partial funding, and Colciencias provided the Ph.D. scholarship funding. We thank avocado producers for valuable information and help during this research. The Alcaldia de Medellin (Antioquia) via its program "Sapiensa" financed the internship of the first author at the University of Kansas. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

References

Agrios G. 2005. Plant Pathology. Elsevier Academic Press. Dana Dreibelbis, London, UK, 952 pp.
APS. 2017. Diseases of avocado (*Persea americana* Miller). Avalaible on: https://www.apsnet.org/publications/commonnames/Pages/Avocado.aspx.
Barnett H.L., Hunter B.B. 1972. Illustrated Genera of Imperfect Fungi. Burgess Publishing Company, Minneapolis, 241 pp.
Barve N., Barve V., Jiménez-Valverde A., Lira-Noriega A., Maher S.P., Peterson A.T., Villalobos F. 2011. The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecological Modelling 222 (11): 1810–1819. DOI: https://doi.org/10.1016/j.ecolmodel.2011.02.011
Bohlen P.J. 2006. Biological invasions: Linking the aboveground and belowground consequences. Applied Soil Ecology 32 (1): 1–5. DOI: https://doi.org/10.1016/j.apsoil.2005.10.001

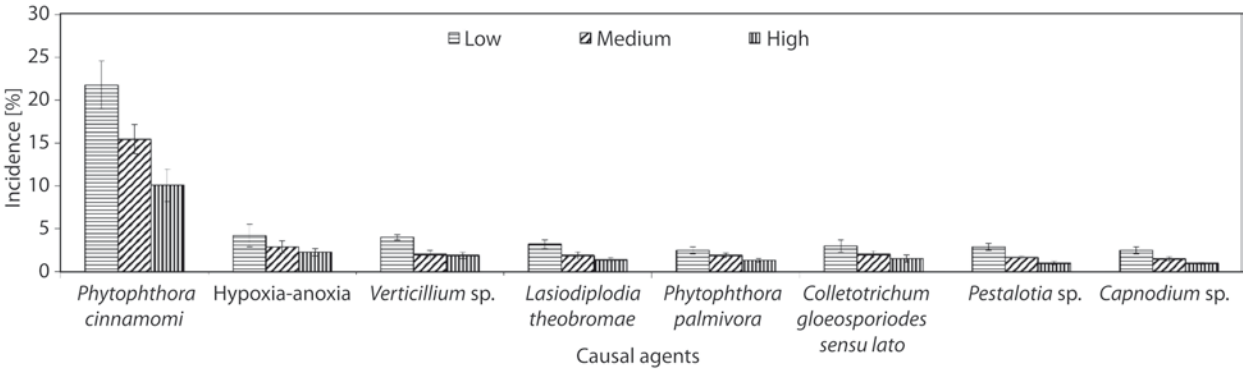

Fig. 7. Relationship between incidences of microorganism associated with Hass avocado disease and technological level of productive system (low, medium and high) – supporting information Figure 1

The bars represent the standard error derived from the residual of deviance statistic of ANAVA. The overlap bars indicate that there are no significant differences between the periods evaluated ($p > 0.05$)

Burgess T.I., Scott J.K., Mcdougall K.L, Stukely M. J., Crane C., Dunstan W.A., Brigg F., Andjic V., Write D., Rutman T., Arentz F., Ota N., Hardy G.E. 2017. Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. Global Change Biology 23 (4): 1661–1674. DOI: https://doi.org/10.1111/gcb.13492

Cochran W. 1977. Sampling Techniques. 3rd ed. John Wiley & Sons, Inc., New York, USA, 448 pp.

Elith J., Phillips SJ., Hastie T., Dudík M., Chee Y.E., Yates C.J. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distribution 17 (1): 43–57. DOI: https://doi.org/10.1111/j.1472-4642.2010.00725.x

Erwin D.C., Ribeiro O.K. 1996. *Phytophthora* Diseases Worldwide. Illustrated edition. American Phytopathological Society, St. Paul, Minnesota, 592 pp.

FAO. 2014. FAOSTAT. Available on: http://www.fao.org/faostat/es/#home. [Accessed: October 24, 2018]

Galdino TV da S., Kumar S., Oliveira L.S.S., Alfenas A.C., Neven L.G., Al-Sadi A.M., Picanço M.C. 2016. Mapping global potential risk of mango sudden decline disease caused by *Ceratocystis fimbriata*. PLoS ONE 11: e0159450. DOI: https://doi.org/10.1371/journal.pone.0159450

Gurgel-Gonçalves R., Galvão C., Costa J., Peterson A.T. 2012. Geographic distribution of chagas disease vectors in Brazil based on ecological niche modeling. Journal of Tropical Medicine: 1–15. DOI: https://doi.org/10.1155/2012/705326

Hardham A.R., Blackman L.M. 2018. *Phytophthora cinnamomi*. Molecular Plant Pathology 19 (2): 260–285. DOI: https://doi.org/10.1111/mpp.12568

Huete A., Didan K., Miura T., Rodríguez E.P., Gao X., Ferreira L.G. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sensing of Environment 83 (1–2): 195–213. DOI: https://doi.org/10.1016/s0034-4257(02)00096-2

Kluza D.A., Vieglais D.A., Andreasen J.K., Peterson A.T. 2007. Sudden oak death: geographic risk estimates and predictions of origins. Plant Pathology 56 (4): 580–587. DOI: https://doi.org/10.1111/j.1365-3059.2007.01602.x

Lu J., Ehsani R., Shi Y., Castro, A.I., Wang S. 2018. Detection of multi-tomato leaf diseases (late blight, target and bacterial spots) in different stages by using a spectral-based sensor. Scientific Reports 8 (1): 2793. DOI: https://doi.org/10.1038/s41598-018-21191-6

Madden L.V., Hughes G., van den Bosch F. 2017. The Study of Plant Disease Epidemics. Saint Paul: American Phytopathological Society, 432 pp. DOI: https://doi.org/10.1094/9780890545058

Malhi Y., Silman M., Salinas N., Bush M., Meir P., Saatchi S. 2010. Introduction: elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. Global Change Biology 16 (12): 3171–3175. DOI: https://doi.org/10.1111/j.1365-2486.2010.02323.x

Menge J.A., Ploetz R.C. 2003. Diseases of avocado. p. 35–71. In: Diseases of Tropical Fruit Crops (R.C. Ploetz, ed.). CABI, Wallingford, 527 pp.

Merow C., Smith M.J., Silander J.A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography 36 (10): 1058–1069. DOI: https://doi.org/10.1111/j.1600-0587.2013.07872.x

Ministerio de Agricultura y Desarrollo Rural de Colombia. 2018. Avocado chain: Indicators and Instruments (Spanish). Available on: https://sioc.minagricultura.gov.co/Aguacate/Documentos/002%20%20Cifras%20Sectoriales/002%20%20Cifras%20Sectoriales%20%202018%20Enero%20Aguacate.pdf#search=Aguacate

Narouei-Khandan H.A., Harmon C.L., Harmon P., Olmstead J., Zelenev V.V., van der Werf W., van Bruggen A.H.C. 2017. Potential global and regional geographic distribution of *Phomopsis vaccinii* on *Vaccinium* species projected by two species distribution models. European Journal of Plant Pathology 148 (4): 919–930. DOI: https://doi.org/10.1007/s10658-017-1146-4

Neerinckx S., Peterson A.T., Gulinck H., Deckers J., Kimaro D., Leirs H. 2010. Predicting potential risk areas of human plague for the Western Usambara Mountains, Lushoto District, Tanzania. The American Journal of Tropical Medicine and Hygiene 82 (3): 492–500. DOI: https://doi.org/10.4269/ajtmh.2010.09-0426

Pearson R.G., Raxworthy C.J., Nakamura M., Townsend A.T. 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34 (1): 102–117. DOI: https://doi.org/10.1111/j.1365-2699.2006.01594.x

Peterson A.T. 2014. Mapping Disease Transmission Risk: Enriching Models Using Biogegraphy and Ecology. Johns Hopkins University Press, Baltimore, Meryland USA, 210 pp. DOI: 10.1353/book.36167

Peterson A.T. 2007. Why not why where: the need for more complex models of simpler environmental spaces. Ecological Modeling 203 (3–4): 527–530. DOI: https://doi.org/10.1016/j.ecolmodel.2006.12.023

Peterson A.T. 2006. Ecologic niche modeling and spatial patterns of disease transmission. Emerging Infectious Diseases 12: 1822–1826. DOI: 10.3201/eid1212.060373

Peterson A.T., Nakazawa Y. 2008. Environmental data sets matter in ecological niche modelling: an example with *Solenopsis invicta* and *Solenopsis richteri*. Global Ecology and Biogeography 17: 135–144. DOI: https://doi.org/10.1111/j.1466-8238.2007.00347.x

Peterson A.T., Papeş M., Soberón J. 2008. Rethinking receiver operating characteristic analysis applications in ecological niche modeling. Ecological Modelling 213 (1): 63–72. DOI: https://doi.org/10.1016/j.ecolmodel.2007.11.008

Peterson A.T., Scachetti-Pereira R., Hargrove W.W. 2004. Potential geographic distribution of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) in North America. The American Midland Naturalist 151 (1): 170–178. DOI: https://doi.org/10.1674/0003-0031(2004)151[0170:pgdoag]2.0.co;2

Peterson A.T., Soberón J., Anderson R., Pearson R., Martínez-Meyer E., Nakamura M., Araújo M. 2011. Ecological Niches and Geographic Distributions. Princeton University Press. 330 pp. DOI: 10.23943/princeton/9780691136868.001.0001

Pettorelli N. 2013. The Normalized Difference Vegetation Index. Oxford University Press, Oxford England, 69 pp. DOI: https://doi.org/10.1093/acprof:osobl/9780199693160.001.0001

Phillips S.J., Anderson R.P., Schapire R.E. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling 190 (3–4): 231–259. DOI: https://doi.org/10.1016/j.ecolmodel.2005.03.026

R Development Core Team. 2017. R: The R Project for Statistical Computing. Available on: https://www.r-project.org/. [Accessed: January 24, 2018]

Ramírez-Gil J.G. 2018. Avocado wilt complex disease, implications and management in Colombia. Revista Facultad Nacional de Agronomía Medellín 71 (2): 8525–8541. DOI: https://doi.org/10.15446/rfna.v71n2.66465

Ramírez-Gil J.G., Gilchrist Ramelli E., Morales Osorio J.G. 2017. Economic impact of the avocado (cv. Hass) wilt disease complex in Antioquia, Colombia, crops under different technological management levels. Crop Protection 101: 103–115. DOI: https://doi.org/10.1016/j.cropro.2017.07.023

Ramírez-Gil J.G., Morales J.G., Peterson A.T. 2018. Potential geography and productivity of "Hass" avocado crops in Colombia estimated by ecological niche modeling. Scientia Horticulturae 237: 287–295. DOI: https://doi.org/10.1016/j.scienta.2018.04.021

Ramírez-Gil J.G., Castañeda D.A., Morales J.G. 2014. Etiological studies of avocado wilt in Antioquia-Colombia

(Spanish). Revista Ceres 61: 50–61. DOI: 10.1590/S0034-737X2014000100007
Sanclemente M.A., Schaffer B., Gil P.M., Vargas A.I., Davies, F.S. 2014. Pruning after flooding hastens recovery of flood-stressed avocado (*Persea americana* Mill.) trees. Scientia Horticuturae 169: 27–35. DOI: https://doi.org/10.1016/j.scienta.2014.01.034
Saupe E.E., Barve V., Myers C.E., Soberón J., Barve N., Hensz C.M., Lira-Noriega A. 2012. Variation in niche and distribution model performance: The need for a priori assessment of key causal factors. Ecological Modelling 237: 11–22. DOI: https://doi.org/10.1016/j.ecolmodel.2012.04.001
Seifert K., Morgan-Jones G., Gams W., Kendrick B. 2011. The Genera of Hyphomycetes. CBS-KNAW Fungal Biodiversity Centre, Utrecht, Netherlands, 997 pp.
Stolzy L., Zentmyer G., Klotz L., Labanauskas C. 1967. Oxygen diffusion, water, and *Phytophthora cinnamomi* in root decay and nutrition of avocados. American Society for Horticultural Science 90: 67–76.
Varela S., Anderson R.P., García-Valdés R., Fernández-González F. 2014. Environmental filters reduce the effects of sampling bias and improve predictions of ecological niche models. Ecography 37: 1084–1091. DOI: https://doi.org/10.1111/j.1600-0587.2013.00441.x
Warren D.L., Glor R.E, Turelli M. 2010. ENMTools: a toolbox for comparative studies of environmental niche models. Ecography 33: 607–611. DOI: https://doi.org/10.1111/j.1600-0587.2009.06142.x
White T., Bruns T., Lee S., Taylor L. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. p. 315–322. In: "PCR Protocols: A Guide to Methods and Applications" (M.A. Innis, D.H. Gelfand, J.J. Sninsky, T.J. White, eds.). Academic Press, San Diego Usa, 482 pp.
Zentmyer G. 1980. *Phytophthora cinnamomi* and Diseases It Causes. Phytopathological Monograph, Phytopathological Society, 96 pp.
Zentmyer G. 1984. Avocado diseases. Tropical Pest Management 30: 677–682.