Coconut lethal yellowing-like diseases: Insights from predicting potential distribution under different climate change scenarios

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Abstract

Coconut is recognized for its popularity in contributing to food and nutritional security. It generates income and helps to improve rural livelihood. However, there is a rise in the number of plant diseases due to globalization, including lethal yellowing-like diseases (LYD). A clear understanding of climate-suitable areas for disease invasion is essential for implementing quarantine measures. Therefore, we modelled in Maximum Entropy to establish habitat suitability of LYD under current and future climate change scenarios using three Shared Socioeconomic Pathways (SSPs) (1.26, 3.70 and 5.85) for three time periods (2041-2060, 2061-2080 and 2081-2100). The area under the curve value for LYD was 0.98, suggesting that the model's performance was very good. The predictor variables that most influenced LYD projections were minimum temperature of the coldest month (88.4%) and the precipitation of the warmest quarter (7.3%). Outside its current range, the model projected climate-suitable areas of LYD in Australia, Asia and South America. Our study highlights potential climate suitable and unsuitable areas of LYD, and provides useful information for increasing quarantine measures. Also, the potential expansion of the disease into uninfected areas suggests that future research should focus on development of resistant or tolerant coconut varieties against the disease.

Introduction

Coconut (*Cocus nucifera* L.) is one of the world's major palms recognized for its popularity in contributing to economic, cultural, food, and social life of some of the world's poorest regions[1]. Coconut-related activities generate income for millions of rural farmers, and play a crucial role in wealth generation and improving the quality of life in tropical areas worldwide. The health benefit of coconut is well documented, especially in the provision of vitamin B, calcium, magnesium, potassium, and dietary fiber. Globally, about 11 million farmers cultivate coconut across 12 million hectares [1,2] in 90 countries and territories, with a total production of 61 million tons in 2016, with which a higher proportion was produced in Indonesia, Philippines and India[3]. In Africa, two million tons of coconut were produced in 2016[3], which appears to be far below the continent's potential capabilities. For instance, Tanzania is the leading coconut producer in Africa, with about 134,068 ha under coconut cultivation, representing 1% of the land in use[4]. Several factors, including lack of certified planting materials, lack of capital, climate change, and pests and diseases, hinder coconut industry's sustainability and profitability[2]. However, diseases are a major constraint, of which lethal yellowing-like diseases of coconut (LYD) is the economically most significant threat to the coconut industry, particularly in the Sub-Saharan Africa (SSA).

The taxonomy of phytoplasmas is based on 16S rRNA sequences, and two parallel classification systems have been developed, the 16Sr group system, based on restriction enzyme digest profiles of the 16S rDNA, and the *'Candidatus* Phytoplasma' species system in which phytoplasmas with less than 97.5% homogeneity of their 16S rRNA gene sequence can be put into other '*Ca.* Phytoplasma' species when they grouped based on their distinctive properties

72 (i.e., biological, phytopathological and genetic) [5]. In the Americas and the Caribbean region, the
73 strain present is referred to as 16SrIV and also known as '*Candidatus* Phytoplasma palmae'. In
74 Africa, there is the 16SrIV-C group on coconut in Tanzania and Kenya[6], and also called '*Ca.*
75 Phytoplasma cocostanzania'. The other strains are in the 16SrXXII group. The 16SrXXII-A strain,
76 known as '*Ca.* Phytoplasma palmicola'[7] is found in Nigeria and Mozambique. In Ghana and Cote
77 D'Ivoire, the phytoplasma that occurs is slightly different, and it is called 16SrXXII-B or '*Ca.*
78 Phytoplasma palmicola' - related strain[8].
79 This diversity and distribution in strains have been attributed to host plants, vectors, and
80 genetic variability[1], suggesting that varying severity of infections associated with the strains
81 may exist in different geographical locations. For instance, in Papua New Guinea, symptoms of
82 Bogia coconut syndrome is similar to that of LYD but without inflorescence necrosis, and attacks
83 are more common in both young and matured palms[9].
84 Lethal yellowing diseases are a group of destructive diseases of coconut and other palms, and
85 pose a huge threat to the coconut industry, wherever it occurs. The disease has accounted for
86 substantial economic losses of 85.54% of coconut trees in Jamaica between 1963 and 1983[10],
87 38% of coconut trees in Tanzania[11], and several millions of coconut trees in Ghana, Nigeria, and
88 Togo[12,13]. For the past decades, globally, lethal yellowing-like diseases have killed millions of
89 palms[14], posing a risk to others. The disease's characteristic symptoms include premature nut
90 drop, inflorescence necrosis, yellowing of fronds, failure to produce nuts, retarded palm
91 growth, and subsequent death of the affected palm.
92 Currently, control of phytoplasma diseases involves tetracycline antibiotics, and this has been
93 useful for a few high value ornamental or palms[12]. However, widespread antibiotic use is not an

environmentally sound policy and the costs are beyond the reach of poor peasant farmers. Hence, antibiotics application in Agriculture in most European countries is banned[15]. The vector of LYD (16Sr IV-A) in the US has been shown to be the planthopper *Myndus crudus* (reclassified taxonomically as *Haplaxius crudus*)[16] but in Africa and other places, the vectors are unknown[1]. Also, there is no effective management of LYD. Current management strategies include the removal of disease-palms, the use of tolerant cultivars, and antibiotic application. The latter appears to be expensive for subsistence coconut farmers. Hence, implementing strict quarantine measures in countries where the disease has not been reported will reduce the spread to uninfected areas. Also, understanding areas at risk of disease invasion will provide a baseline information for policymakers.

Species distribution modeling has been useful for predicting suitable areas for crops[17], insects[18,19], birds[20,19] Plant diseases[21], vectors of human importance[22] and agriculture ecosystems[23]. Climate change can either directly or indirectly affect the distribution and abundance of plant pathogens. In the past years, globally, there has been an increase in the average surface temperature of 0.2 ^{o}C every 10 years[24]. Climate change can affect crop protection chemical effectiveness, host resistance to pathogens, and microbial interactions[25]. Hence, modeling areas at risk of invasion is crucial for developing and implementing appropriate management strategies[26].

Species distribution models have been used to simulate the potential impact of plant pathogens for decision making and mitigation[27,28], plants[28], human diseases[29]. However, the effect of climatic conditions on phytoplasma changes is poorly documented[30]. Up to date, there is no study on the impact of climate change on LYD and its main host palm for appropriate

quarantine measures. Therefore, to classify and forecast possible distribution of LYD under varying climate change scenarios, we used maximum entropy (MaxEnt) to establish the habitat suitability for both the disease and its main host palm.

RESULTS

Climate variables that constrain lethal yellowing-like diseases and coconut model

Our analysis of climate variable contribution to the current LYD model showed that the minimum temperature of the coldest month (bio6, 88.4%) was the most important factor, affecting LYD model performance (Table 1).

Table 1. The bioclimatic variables used in lethal yellowing-like diseases of coconut in MaxEnt model, and the average percent contributions of the bioclimatic variables.

Bioclimatic variable	Percentage contribution	Permutation importance
bio6	88.4	87.4
bio18	7.3	2.4
bio15	2.2	1.9
bio4	2.2	8.4

Other factors that contributed to the model were precipitation of warmest quarter (bio18, 7.3%), precipitation seasonality (bio15, 2.2%), and temperature seasonality (bio4, 0.5%). Minimum temperature of the coldest month and temperature seasonality showed a total contribution of 90.6% for LYD. Whereas, precipitation seasonality and precipitation of the warmest quarter contributed less than 5% to the model, suggesting that thermal conditions much more than precipitation appear to be the main factors influencing LYD distribution globally. Our results

showed that the minimum temperature of the coldest month was the most important climatic variable that influenced the crop model performance (bio6, 85.9%), followed by temperature seasonality, precipitation of the warmest quarter and then precipitation seasonality in descending order of variable contribution (Table 2). Minimum temperature of the coldest month and temperature seasonality combined contributed 94.6% to the crop's model performance. Precipitation seasonality and precipitation of warmest month contributed less than 5.5% to the model. Also, indicating that temperature much more than precipitation influenced the distribution of coconut.

Table 2. The final bioclimatic variables used in coconut MaxEnt model, and the average percent contributions of the bioclimatic variables in the crop distribution model.

Bioclimatic variable	Percentage contribution	Permutation importance
bio6	85.9	88.1
Bio4	8.7	5.6
bio18	4.7	5.3
bio15	0.7	1.0

Potential suitable areas of lethal yellowing-like diseases and coconut under current scenario

The area under the curve (AUC), which provides important information on the MaxEnt model performance was used to assess how well LYD distribution was predicted. The disease model AUC value was 0.9836 (>0.5 of a random model), suggesting a high level of accuracy in the model simulation. Our predicted-areas of the disease habitat suitability exceeded its current distribution, with highly habitat suitability in the coastal regions (Fig. 1).

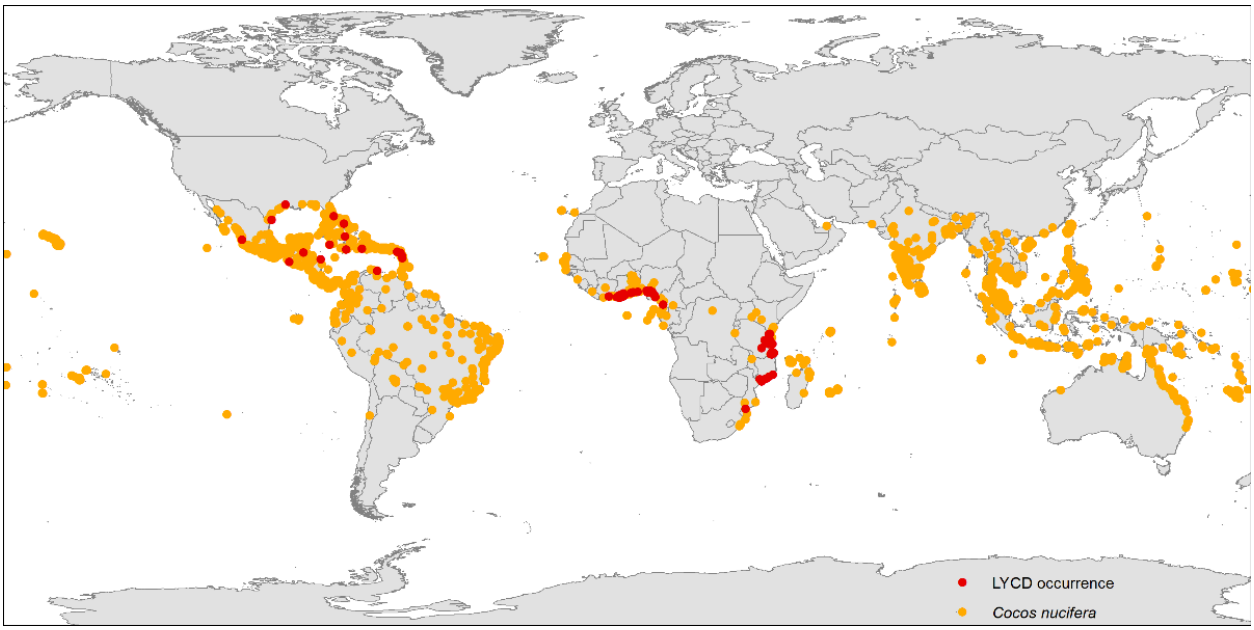


Figure 1: Occurrence data of LYD in comparison to GBIF occurrence records for *Cocos nucifera*. The base map was created using ESRI ArcMap.

The potential climate suitable area of LYD were mainly distributed in South America, West Africa, East Africa, South Asia and South East Asia (Fig. 2 and 3).

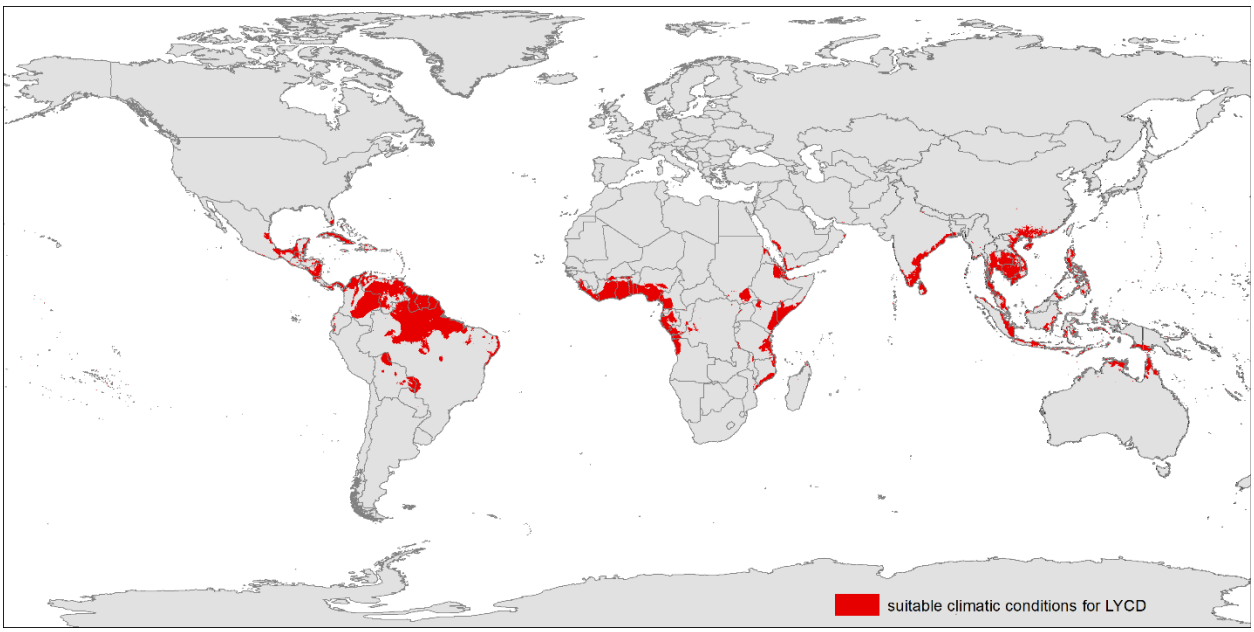


Figure 2: Area with modelled climatic suitability for LYD. Dichotomous results applying the equal sensitivity and specificity threshold. The base map was created using ESRI ArcMap

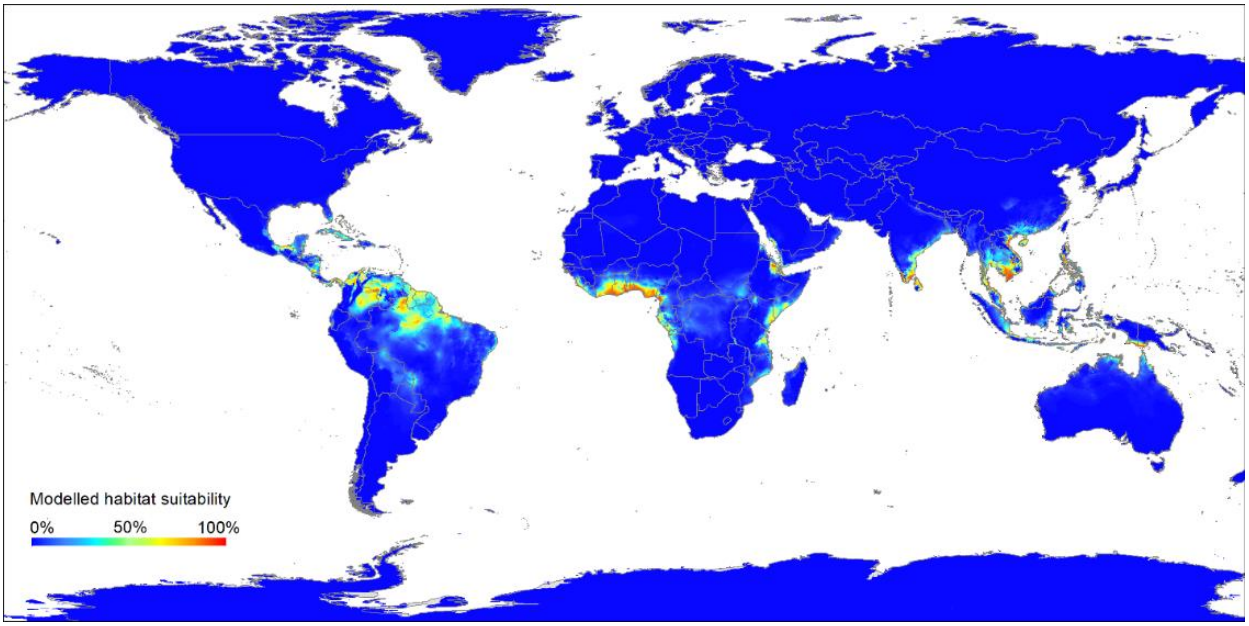


Figure 3: Modelled climatic suitability for LYD. Based on occurrence data (reduced to only one occurrence record per 2.5 arc min grid cell at maximum) and four only little intercorrelated bioclim variables (bio15, bio04, bio06, bio18) modelled on a global scale, MaxEnt model with LQP features only. The base map was created using ESRI ArcMap.

In addition, habitat suitability was observed in Australia and Indonesia. The countries highly suitable for the disease in Africa stretches from the coastal regions of Senegal through Ghana to Angola. Other African countries found to be suitable for LYD in Africa were Kenya, Somalia, Djibouti, Tanzania and Eritrea. In the Southern America, the climate suitable areas included Brazil, Guyana, Venezuela, Suriname and French Guiana, whereas the coastal areas of India were suitable for the disease in South Asia. Our current prediction highlighted Bangladesh, Thailand and Burma as climate suitable areas for LYD, especially in the coastal regions. Overall, our projection exceeded the current distribution of the disease.

The model forecasted more climate suitable areas for the crop outside its current range (Fig. 4).

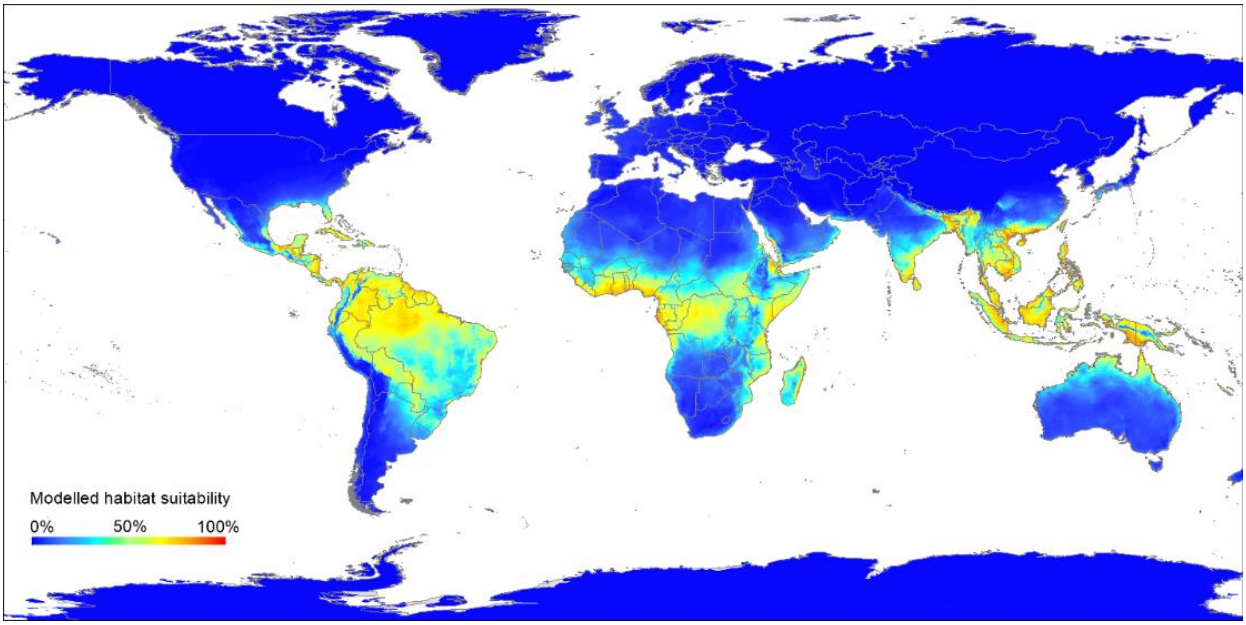


Figure 4: Modelled climatic suitability for *Cocos nucifera.* Based on GBIF occurrence data and four only little intercorrelated bioclim variables (bio15, bio04, bio06, and bio18) modelled on a global scale, MaxEnt model with LQP features only. The base map was created using ESRI ArcMap.

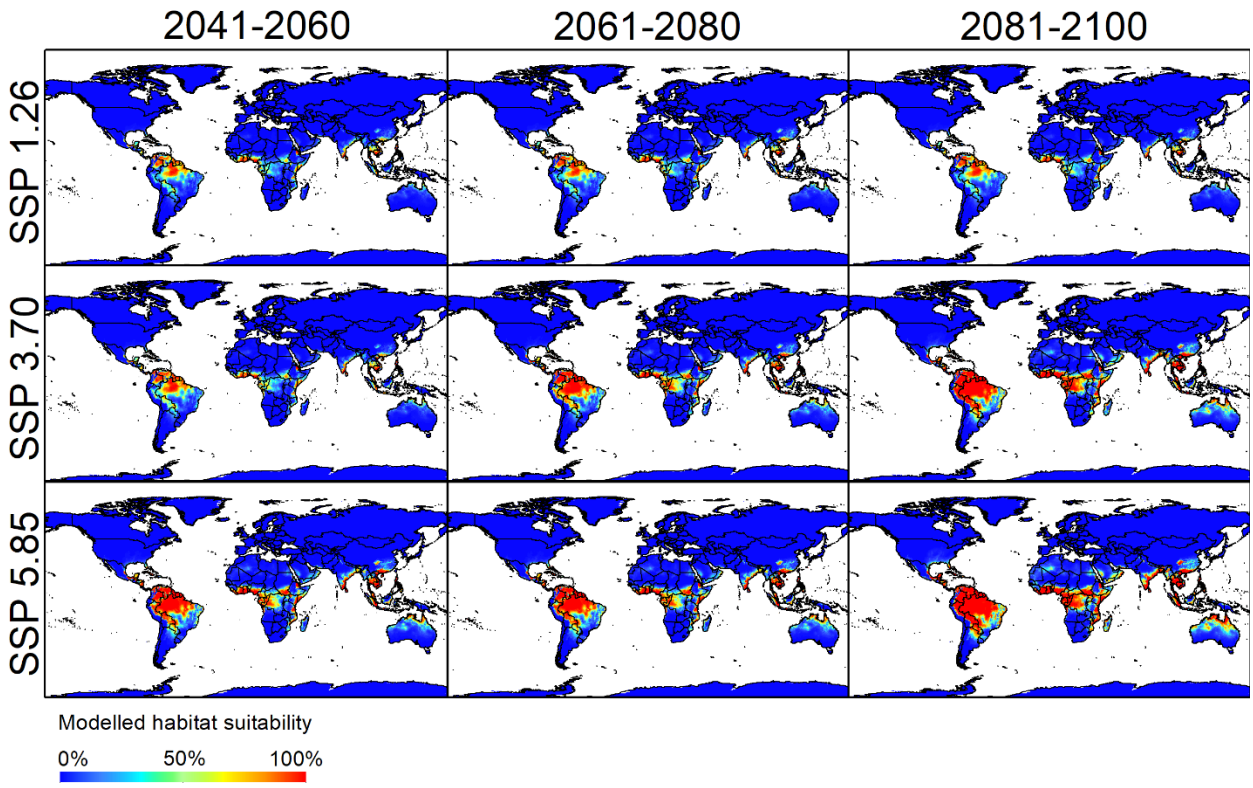
The performance of the model was very good with AUC of 0.8723, which is higher than 0.5 of a random model. Areas projected to be climate suitable for the crop cultivation were outside its

current distribution in Western and Central Africa, coastal regions of South and South East Asia, and the Guianas and Brazil in South America, and in North America. However, the suitable areas for coconut cultivation was observed in all the continents except Antarctica and Europe, which appear to be unsuitable for the coconut cultivation. In addition, the distribution of coconut was greater than that of LYD, suggesting that areas not suitable for the disease is suitable for the cop production.

Projection of suitable areas of lethal yellowing-like diseases of coconut-future scenarios

The MaxEnt model predicted LYD future distribution for three Shared Socio-economic Pathways (SSPs) (1.26, 3.70 and 5.85) (Fig. 5). A shift in LYD distribution from the current to future predictions was observed, as shown by the different hotspots in the affected areas. For the low climate change scenario (SSP1.26), there was no clear expansion of climate suitable areas of LYD from 2041-2060 to 2081-2100. The highly suitable areas of LYD in Africa stretches from Côte D'Ivoire through Ghana to Nigeria. The hotspots in South and South East Asia were along the coastal belts. However, in South America, there was an inland expansion of climate suitable areas of LYD, and the major areas at risk of spread were Brazil and the Guianas. Under the moderate climate change scenario (SSP3.70), there was consistent expansion of LYD suitable areas into new areas from 2041 to 2100. The highly suitable areas included South America, West Africa and Central Africa. The extreme scenario (SSP 5.85) showed an increase in potential climate-suitable areas of LYD from 2041-2060 to 2081-2100. Climate suitable areas that showed expansion of suitable areas were in the South America, Africa and Australia. However, most of the areas affected were areas in the coastal belt. Compared with the current scenario, there

218 was a significant expansion to the inland regions of many LYD-affected countries. For the
219 extreme climate change scenario, areas which were not suitable in the low and moderate
220 climate change scenarios were highly suitable in the extreme scenario, especially in the in the
221 coastal regions.



222
223 Figure 5: Projected climatic suitability for LYD under future climatic conditions. The base maps
224 were created using ESRI ArcMap.
225
226
227 **Projection of suitable areas of coconut-future scenarios**
228
229 Under the low climate change scenario (SSP1.26), there was an expansion of areas suitable for
230 coconut cultivation from 2041-2060 to 2081-2100 (Fig. 6). The areas projected to be highly
231 suitable under the low climate change were Brazil, coastal areas of west and East Africa and
232 South East Asia. Our analysis showed that climate suitable areas increased across the different

time periods, especially in Central Africa, West Africa and South America under the moderate climate change scenario (SSP3.70).

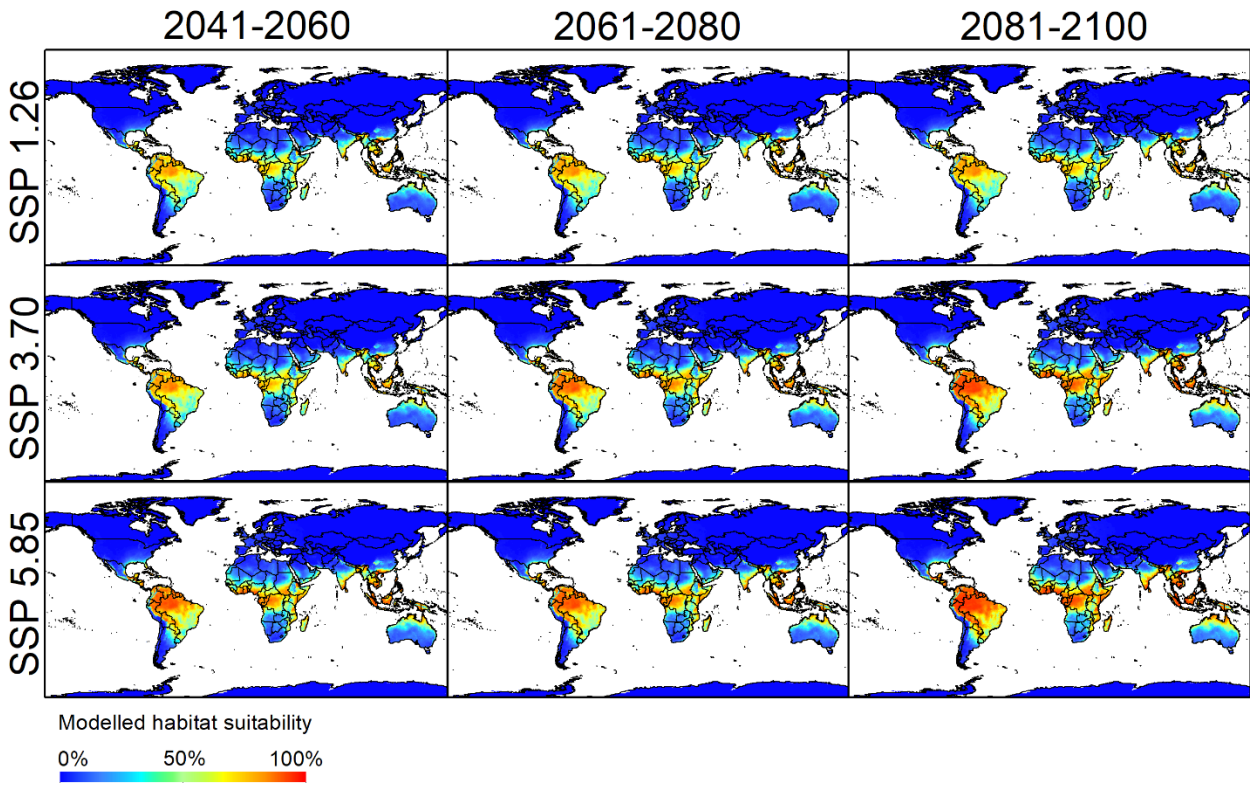


Figure 6: Projected climatic suitability for *Cocos nucifera* under future climatic conditions. The base maps were created using ESRI ArcMap.

In addition, there were highly suitable areas in South Asia and South East Asia, which increased across the three different time periods. There was an increase climate suitable areas for coconut in Côte d'Ivoire, Gabon, Angola and Ghana. For the extreme climate change scenario (SSP5.85), an inland shift and expansion in coconut habitat suitability were depicted in the disease hotspots. The coastal belt of most regions had optimal suitable areas of the coconut. Also, the habitat suitability of coconut increased from 2041-2060 to 2081-2100. Our analysis showed that Europe and Antarctica appear to be unsuitable for coconut. There was an expansion of suitable areas in the Central and Eastern, with a marginal reduction of highly

suitable areas in the Western Africa. Also, Madagascar and Australia showed a slight expansion of climate-suitable areas for coconut, suggesting possible future expansion of the crop in the region.

DISCUSSION

Lethal yellowing diseases attack over 30 palms[31], with coconut most severely affected[1]. It poses a serious threat to the coconut industry, especially in Africa[32]. For instance, Tanzania, which is the leading producer of coconut in Africa, with the fourth-largest cultivation area has low production due to the disease[33], and the severity of its dry season[34]. Attempts to control LYD ad prevents its spread to clean regions involved the use of tetracycline injection through coconut trunk [35,36], on-farm quarantine, strict regular surveillance, cutting down and burning of symptomatic palms, replanting high yield and LYD resistance coconut varieties, whole-farm weed control and a good fertilization regime[37]. Nevertheless, these methods appear to be expensive, so there is no ecologically sound management strategy for the disease. Another way, is to develop and implement quarantine measures aimed at preventing the spread of the disease to uninfected areas. Hence, for the first time, we have established climate suitable areas for surveillance and monitoring of the disease, especially in areas that the disease has not been reported.

However, a clear understanding of the degree to which climate change can significantly impact potential plans in managing and developing control measures, especially identifying where disease pathogens can pose a serious threat to the coconut industry is crucial. By using

modeling methods relevant to the data available on lethal yellowing-like diseases of coconut, we have identified broad-scale trends that provide insight into the significance of thermal conditions and rainfall that could determine the distribution of the most devastating disease of coconut in Africa. Our projections have highlighted either climate-suitable or unsuitable for potential LYCD current and future invasion, which is useful for developing preventive measures against the disease. Lethal yellowing diseases affected palms produced more symptoms in cooler months of the year, but it was not known if this corresponded to earlier infestations or just more suitable periods for symptoms to develop[38]. Furthermore, seasonality has been associated with lethal yellowing, with some seasons more favourable to the disease infestation than others[39]. We found that the minimum temperature of the coldest month and mean temperature of the coldest quarter were the main factors influencing the habitat suitability of LYD, with minimum temperature of the coldest month contributing to most of the model. An earlier study, investigating the influence of temperature and carbon dioxide on phytoplasmas, observed a faster phytoplasma multiplication under cooler conditions in putative vectors[40.] Also, implicated weather conditions in LYD putative vectors feeding and dispersal behaviour[41]. Phytoplasma-associated diseases may increase due to global warming / climate change, which is beneficial to cold-sensitive phytoplasma vectors, as well as the application of new and more restrictive regulation on the use of many pesticides for the control of phloem-feeding insects and the growth in organic farming [42]. Hence, detection of phytoplasma will therefore become increasingly important in the future.

Because the disease and the host plant overlapped in our projections, some countries in Africa (i.e., Ghana, Kenya, Cote D'Ivoire, Togo, Gabon and Somalia) South America (i.e., Brazil, Guyana,

291 Venezuela and Colombia), Asia (i.e., southern India, Cambodia, Sri Lanka, Sumatra and Thailand)
292 and Australia (i.e., areas include Northern part of western Australia, Northern territory and
293 Queensland) are at risk to the disease, future damage to the crop as a result of the disease
294 severity requires climate mitigation policies to allow quarantine measures to be put in place to
295 prevent its spread to disease-free zones. Our results showed that coconut is widely distributed,
296 especially in Africa and South America and there is a potential expansion of climate-suitable
297 areas in future. Given that coconut is an important crop in Africa[43], America[44] and Asia[45], should
298 habitat suitability increase coupled with increased production, there will be more jobs, income
299 generation among the rural livelihood. In addition, availability of coconut products such as oil,
300 milk and water as staple food sources[46] will help ensure food security. Without coconut, living
301 on some coastal regions will be unsustainable, as not only does coconut serve as a main source
302 of food but also used in construction of houses, and coconut shells are used for popular
303 household products including bowls and fuel[47]. A variety of value-added goods from coconut
304 are processed. Hence, changes in coconut production could bring social and economic benefits
305 to some of the world's poorest regions. Therefore, any disease outbreak, especially LYD, would
306 cause environmental and economic upheavals.
307
308 An outbreak of LYD in Côte d'Ivoire, for instance, destroyed more than 350 ha of plantations,
309 resulting in the loss of 12,000 tons of copra per year and, threatening another 7000 ha[8]. The
310 production of cash crop for exports and domestic consumption has been associated with rural
311 poverty alleviation and growth support in many developing countries. Coconut do not yield
312 nuts until several years after replanting, hence farmers should intercrop coconut with buffer

crops such as cowpea, maize and pepper, especially in the LYD hotspots. Because coconut is an important crop, significant crop losses due to LYD and the resulting lack of revenue would lead to more rural farmers heading to urban areas, which would intensify rural poverty[48] in future.

Several studies on putative vectors of LYD have been inconclusive because they failed to confirm the successful transmission of LYD from diseased-palms to healthy ones [32,43]. However, many insects have been implicated in the spread of the disease. For instance, the planthopper *Haplaxius crudus* Van Duzee, has been reported in Mexico[49], *Nodoterpa curta* in Côte D'Ivoire[50], *Platacantha lutea* Westwood and *Diostrombus mkurangai* Wilson in Mozambique and Tanzania[41,51,52] in Ghana [53]. The outbreak of LYD is marked with initial symptoms occurring in one or two palms followed by sporadic cases up to 100 m away from the primary infection, then further spread to few kilometers to about 100 km, which can be followed by a "jump" to anywhere [43,54]. The spread rate often appears to be irregular, with peaks occurring in a few months but not consistent in all coconut growing regions. Inconclusive results of vector identification coupled with the nature of disease spread, suggest that quarantine measures using output from our present study would help mitigate its spread to clean areas.

Attempts to simulate LYD spread are difficult on a small scale[54], but have been conducted on larger scales[55]. Geographic features such as mountain ranges, which may not allow vectors cross naturally, could affect the disease spread[56]. Anthropogenic activity appears to be a substantial cause of LYD spread through movement of plant materials and farm machinery. For example, grasses and palm trees imported from Florida to Mexico for new golf courses were

implicated in harbouring vector species in the 1980's[57]. Many crops have a similar history of phytoplasma-associated diseases spread by human help[58]. But phytoplasmas have not been detected in embryo-derived seedlings *in-vitro*, hence, there is no indication of transmission of phytoplasmas to the progeny palms for disease spread, through transport of planting materials[59].

Although thermal conditions played a crucial role in the distribution of the suitable areas, precipitation was among the four factors that strongly constrained the disease model. Our projection showed that high habitat suitability in the coastal regions, which is consistent with that of [43], who reported a high incidence of LYD in Ghana's coastal regions (i.e., Western, Central and Volta). Other studies have also reported LYD in coastal areas of coconut-growing regions[12,60]. The higher LYD incidence in the coastal regions could be attributed to soil characteristics and higher number of palms in the coasts. However, the effect of coastal soil characteristics on LYD distribution requires is poorly understood.

There is a significant effect on the rate at which climate change influences the spread and establishment of vectors and pathogens in areas originally considered unfavourable [30,61]. An increase in temperature of 1 °C could change ecological zones by up to 160 km[62]. Also, increased temperatures can trigger a shift in insects' ecological niche into new areas[63] and even new countries. However, the ability of a species to establish outside its native niche is determined by several factors: such as natural enemies (predators, parasitoids and fungi), vegetation, and host plant presence, as well as anthropogenic activities. Therefore, to clearly

understand the ecology and possible risk of spreading this destructive disease through different coconut agroecosystems, all these factors need to be further investigated.

High temperatures increase the rate of dispersal of certain phytoplasmas by faster multiplication in the host or higher feeding frequency of insect vectors, resulting in increased transmission possibilities[64]. Apart from temperature, climate change is closely linked with an increased occurrence of drought and storms that can increase plant stress[65], exposing them to pests and disease attacks. Hurricanes could be associated with high incidence of LYD in the Caribbean.

All presence-only data used for the MaxEnt model were obtained from secondary sources; except for Ghana. Therefore, the research corresponds to the definition advocated by the Open Science movement, which encourages data reuse for further exploration and decisions[66]. Models that only use presence-only data are easier to build and are common than those that jointly use input presence and absence data[67]. Presence data are usually easier to collect because confirming an organism's absence requires comprehensive and thorough surveys. Also, it may be difficult or costly to obtain such presence-absence data.

CONCLUSION

For the first time, we have established the suitable and unsuitable habitats of the most devastating coconut disease worldwide using bioclimatic variables. Our model performance was very good and reliable based on the current distribution of the disease in the four continents. The simulated LYD, would help to better understand the impact of climate change on the disease spread. Such finding is very crucial as it serves as an early warning for coconut-

379 producing regions, where LYD is still not present. Plant control approaches focused on potential
380 habitat suitability of plant disease will be an essential part of the integrated production disease
381 management systems.
382
383 ## Materials and methods
384 **Disease occurrence data**
385 A survey was conducted in Ghana between August 2017 and February 2020 to determine areas
386 affected by LYD (Table S1). Global Positioning System (GPS) coordinates (latitude and longitude)
387 of fields affected by the disease were recorded. Coconut phloem tissues in the form of sawdust
388 were collected following the protocol of[59]. To obtain genomic DNA for LYD diagnosis, 1.0 g of
389 coconut tissue was ground in 5 ml of CTAB (20Mm EDTA Ph 8.0, 1.4 M NaCl, 100 mM Tris-HCl
390 pH 8.0, 2% Cetyl trimethylammonium bromide) with a sterilized lab mortar and pestle into a
391 fine suspension. The plant extract (1ml) was transferred into a 2.0 ml Eppendorf tube and
392 incubated at 65 ^{o}C for 30 minutes in a water bath. DNA was then extracted using phenol:
393 chloroform: isoamyl alcohol (25:24:1) and precipitated with isopropyl alcohol following the
394 protocol of[68].
395
396 **DNA Clean-up with PVPP**
397 To clean the DNA, we used a Micro-Bio-Spin column with choroform-isoamyl alcohol protocol
398 or poly (vinyl polypyrrolidone) poly, PVPP powder: micro Bio-Spin Chromatograph column
399 (3cm) and snap off the thin flap. With the lid removed, the column was placed in a 1.5 ml
400 Eppendorf tube. The bottom thin spin column section 2/3 of the way up was filled with PVPP

powder. Afterwards we added 400uL of sterile deionized water and in a benchtop microfuge it was centrifuged for 3 min at 1000 g. The flow-through was discarded. The column was then filled with 200uL of sterile deionized water and centrifuged for 3 min at 1000 g. The column was transferred with the lid removed into a clean-labeled 1.5 ml Eppendorf tube. The extract of DNA was added to the column, centrifuging for 3 min at 1000 g. The cleaned-up DNA was transferred into a new labelled tube in Eppendorf. Normally one round of clean-up is enough to remove PCR inhibitors from a sample of DNA.

Conventional PCR

For all polymerase chain reactions (PCR), 50–100 ng of sample DNA template was added to a 25uL reaction. PCRs were carried out using MangoMix (Bioline, UK) containing: Mango Taq™ polymerase, dNTPs, red and orange reference dyes and Mg^{2+}. A forward and reverse primer at a final concentration of 0.2 µM was used in the reaction. For the detection of the LYD phytoplasma, the primers: CSPWDSecAFor2 / CSPWDSecARev2 [69] were used. The PCR cycling was as follows: one cycle at 94 °C for 3 min, followed by 35 cycles of 94 ° C for 40 s, 55 °C for 40s and 72 °C for 1 min 40s; and 1 cycle at 72 °C for 10 min. Five microliters of each of the PCR products were separated in a 1.5 % agarose gel and visualized with SYBR Safe DNA Gel Stain (Invitrogen, USA) in a UV transilluminator. Approximately 300bp fragments were obtained for positive tests.

Collection of other LYD and coconut presence data

Lethal yellowing-like diseases of coconut historical presence records except Ghana were obtained from peer-reviewed articles and the Centre for Agriculture and Bioscience International (CABI) website (www.cabi.org) (Table S1). Keywords used for the search included both scientific and local names of the disease: Akwa wilt, Cape St. Paul Wilt, Kain-cope disease, lethal disease, lethal decline, lethal yellowing, lethal yellowing disease and lethal yellowing-like diseases. In case, a village or areas was mentioned, google earth engine (https://www.google.com/earth/) was used to obtain the respective latitude and longitude of disease incidence (Table S1). Overall, we compiled 184 occurrences points, the duplicates and presence records in a close proximity were cleaned and reduced 129 records prior to analysis to correct for spatial autocorrelation (i.e., only one occurrence record per grid cell 2.5 arc minutes at maximum), and used for the LYD MaxEnt modelling. For coconut presence-only data, we downloaded the occurrence records provided by the global biodiversity information facility (GBIF) (https://doi.org/10.15468/dl.hy3per). First, we removed all data with latitudes outside the range of -30° to 30°, with the assumption that records outside this range refer to individuals in e.g., greenhouses). The data were then adjusted to the grid of environmental data with only one occurrence record per grid cell 2.5 arc minutes at maximum, resulting in 2,652 occurrence records for the crop.

Environmental data

The bioclimatic data comprise 19 variable layers obtained from the WorldClim database (http:/www.worldclim.org)[70] at 30 seconds (~1 km^2) resolution (Table 3). The seasonal

variation, monthly temperature, monthly precipitation, and extreme climatic indices, were used to calculate the climatic variables. Climatic variables are commonly used for modelling disease suitability due to its direct influence on species distribution, and being more transferrable, whereas the other variable used for modelling have indirect influence on species, and are less transferrable (e.g., land)[71]. With the occurrences and bioclimatic data, we checked the potential collinearity among the stack of bioclimatic variables; there was no need for resampling the layers because they already had all the similar properties. The study of the collinearity was done using the R-package virtual species[72] in R software version 3.6.1[73]. The inbuilt function removes collinearity from the package to analyze the correlation of environmental variable using the Pearson's R method and then provide the vector with the names of variable that are not collinear. Using this function, it is also possible to group the variable layers according to their degree of collinearity (Fig. S1). Out of the 19 bioclimatic layers, four were not collinear and were used in the MaxEnt model (Table 3).

Table 3. The bioclimatic variables that were considered in the MaxEnt model. Bold font indicates the bioclimatic variables used in the final model.

Bioclimatic variable	Unit	Code
Annual mean temperature	°C	bio1
Mean diurnal range in temperature	°C	bio2
Isothermality	°C	bio3
Temperature seasonality (SD× 100)	**°C**	**bio4**
Maximum temperature of warmest month	°C	bio5
Minimum temperature of coldest month	**°C**	**bio6**
Temperature annual range	°C	bio7
Mean temperature of wettest quarter	°C	bio8
Mean temperature of driest quarter	°C	bio9
Mean temperature of warmest quarter	°C	bio10
Mean temperature of coldest quarter	°C	bio11
Mean annual precipitation	mm	bio12
Precipitation of wettest month	mm	bio13
Precipitation of driest month	mm	bio14
Precipitation seasonality	**mm**	**bio15**
Precipitation of wettest quarter	mm	bio16
Precipitation of driest quarter	mm	bio17
Precipitation of warmest quarter	**mm**	**bio18**
Precipitation of coldest quarter	mm	bio19

The final environmental variables were minimum temperature of coldest month (bio6), precipitation of warmest quarter (bio18), precipitation seasonality (bio15), and temperature seasonality (bio4). For future projections, data according to the CNRM-ESM2-1 Global Circulation model[74] for three Shared Socioeconomic Pathways (SSPs); 1.26, 3.70 and 5.85 and three the time periods; 2041-2060, 2061-2080, 2081-2100. Global extent, spatial resolution of 2.5 arc minutes (~ 5*5km^2). All maps were created using ESRI ArcMap.

MaxEnt Model

Maximum entropy (MaxEnt) software[75] is a machine learning program that predicts the probability distribution of an individual species occurrence. There are many approaches for modeling and understanding areas that are ideal habitats for plant diseases, based on the presence or absence of species. Maximum entropy is one of the most commonly used approaches for projecting the species suitability outside its current range based on species presence-only data. It is useful for ecologists, protectionists, and conservationists to forecast areas at risk of pests or disease establishment. We used the MaxEnt modelling approach to predict the habitat suitability of LYD potential distribution because it has proven to be efficient in earlier and recent studies for predicting areas of habitat suitability of species, and a moderate number of parameters favours the performance of the model[76]. The area under the ROC curve (AUC), which measures the quality of the sites ranking[77] was used to evaluate the performance of the MaxEnt model. The area under the curve value of 0.5 (random ranking), 1.0 (perfect ranking), whereas AUC values greater than 0.75 indicates high model performance[78]. There were 2539 training samples and 1.108 training gains for coconut, whereas 145 training samples and 2.8971 regularized training were used for LYD.

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ACKNOWLEDGEMENT

We gratefully acknowledge the financial support for part of this research by European Union's Horizon 2020 research and innovation programme under, project "Insect-borne prokaryote-associated diseases in tropical and subtropical perennial crops" TROPICSAFE grant agreement No. 727459.

AUTHOR CONTRIBUTION

Author's contribution: O.F.A., M.D., H.L.., N.Y. and L.A. initiated the study; S.C., R.G., Y.A., E.T., F.K.A., H.L., F.D., J.O., H.L. and O.B. conceived and designed the experiments; O.F.A., R.G., M.D. and N.Y. contributed materials; S.C., O.F.A. and R.G. analyzed the data: S.C, O.F.A., N.Y., R.G. wrote the paper; all authors revised the manuscript.

CONFLICT OF INSTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raster layers of the models are available from the corresponding author upon request for research or application purposes, subject to approval from the co-authors. The data for analysis are attached as supplementary information.

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