

# Coconut Lethal Yellowing-Like Diseases: Insights From Predicting Potential Distribution Under Different Climate Change Scenarios

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1 **Coconut lethal yellowing-like diseases: Insights from**  
2 **predicting potential distribution under different climate**  
3 **change scenarios**  
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29

30 **Abstract**

31 Coconut is recognized for its popularity in contributing to food and nutritional security. It  
32 generates income and helps to improve rural livelihood. However, there is a rise in the number  
33 of plant diseases due to globalization, including lethal yellowing-like diseases (LYD). A clear  
34 understanding of climate-suitable areas for disease invasion is essential for implementing  
35 quarantine measures. Therefore, we modelled in Maximum Entropy to establish habitat  
36 suitability of LYD under current and future climate change scenarios using three Shared  
37 Socioeconomic Pathways (SSPs) (1.26, 3.70 and 5.85) for three time periods (2041-2060, 2061-  
38 2080 and 2081-2100). The area under the curve value for LYD was 0.98, suggesting that the  
39 model's performance was very good. The predictor variables that most influenced LYD  
40 projections were minimum temperature of the coldest month (88.4%) and the precipitation of  
41 the warmest quarter (7.3%). Outside its current range, the model projected climate-suitable  
42 areas of LYD in Australia, Asia and South America. Our study highlights potential climate  
43 suitable and unsuitable areas of LYD, and provides useful information for increasing quarantine  
44 measures. Also, the potential expansion of the disease into uninfected areas suggests that  
45 future research should focus on development of resistant or tolerant coconut varieties against  
46 the disease.

47

48

49

## 50 **Introduction**

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

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

72 (i.e., biological, phytopathological and genetic)<sup>5</sup>. 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<sup>6</sup>, 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*'<sup>7</sup> 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<sup>8</sup>.

79 This diversity and distribution in strains have been attributed to host plants, vectors, and  
80 genetic variability<sup>1</sup>, 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<sup>9</sup>.

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<sup>10</sup>,  
87 38% of coconut trees in Tanzania<sup>11</sup>, and several millions of coconut trees in Ghana, Nigeria, and  
88 Togo<sup>12,13</sup>. For the past decades, globally, lethal yellowing-like diseases have killed millions of  
89 palms<sup>14</sup>, 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<sup>12</sup>. However, widespread antibiotic use is not an

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

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

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

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

119

## 120 **RESULTS**

### 121 **Climate variables that constrain lethal yellowing-like diseases** 122 **and coconut model**

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

126

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

129

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

130

131 Other factors that contributed to the model were precipitation of warmest quarter (bio18, 7.3%),  
132 precipitation seasonality (bio15, 2.2%), and temperature seasonality (bio4, 0.5%). Minimum  
133 temperature of the coldest month and temperature seasonality showed a total contribution of  
134 90.6% for LYD. Whereas, precipitation seasonality and precipitation of the warmest quarter  
135 contributed less than 5% to the model, suggesting that thermal conditions much more than  
136 precipitation appear to be the main factors influencing LYD distribution globally. Our results

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

145

146 Table 2. The final bioclimatic variables used in coconut MaxEnt model, and the average percent  
147 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

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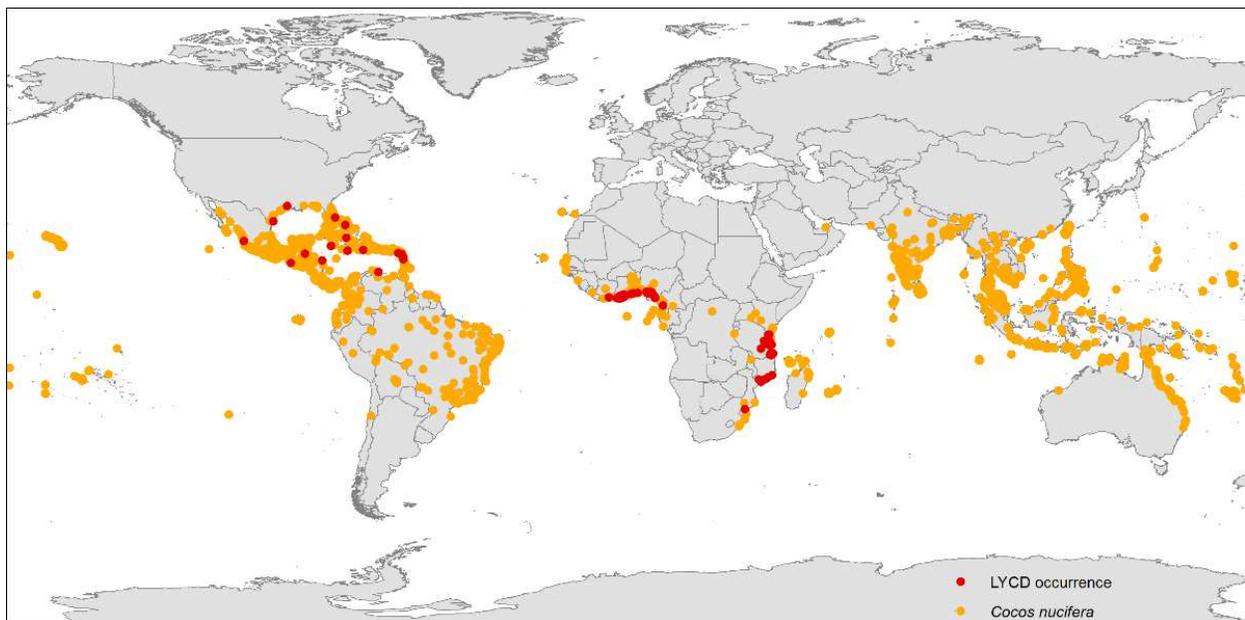
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152

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

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

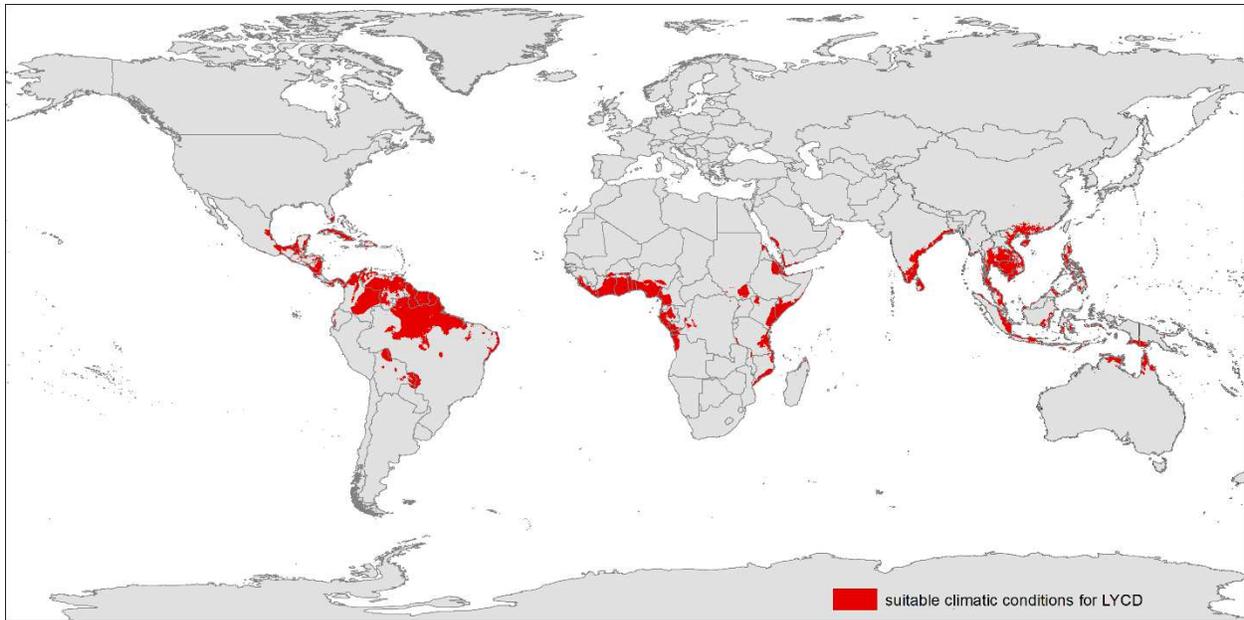
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161  
162 Figure 1: Occurrence data of LYD in comparison to GBIF occurrence records for *Cocos nucifera*.  
163 The base map was created using ESRI ArcMap.

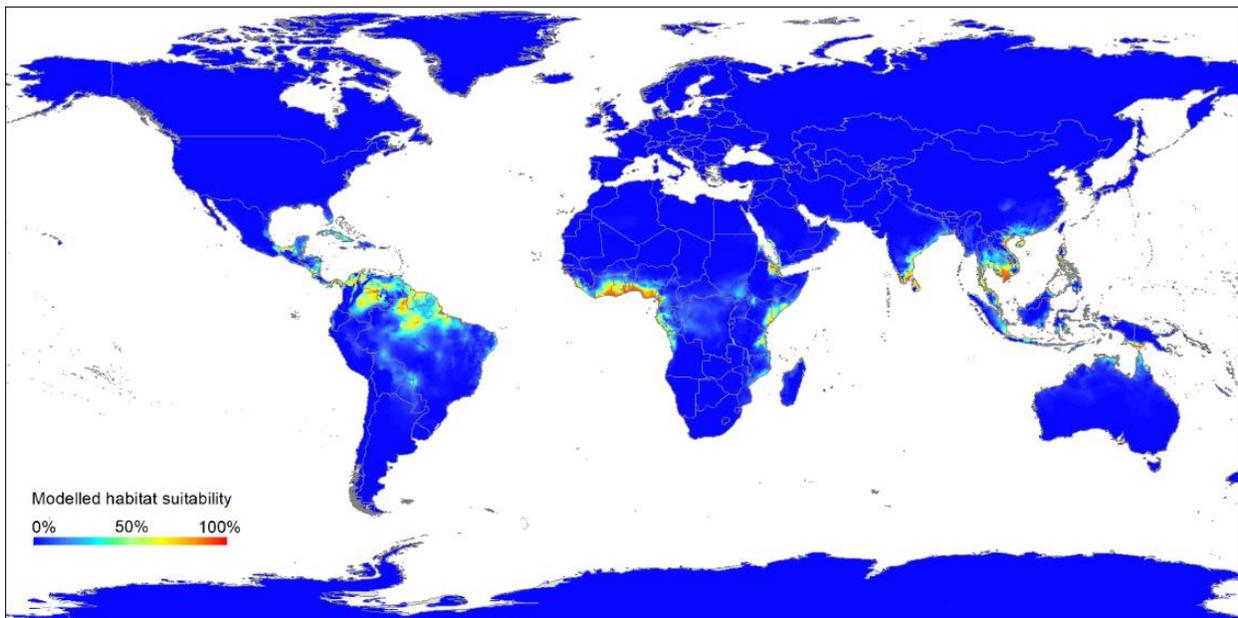
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165 The potential climate suitable area of LYD were mainly distributed in South America, West  
166 Africa, East Africa, South Asia and South East Asia (Fig. 2 and 3).



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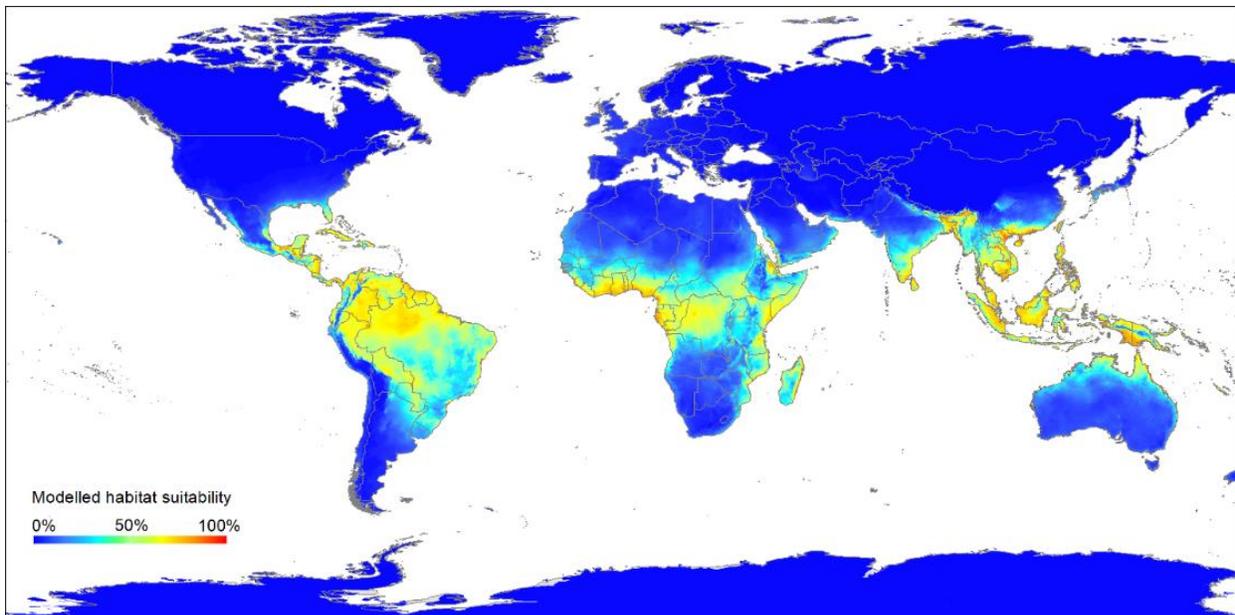
Figure 2: Area with modelled climatic suitability for LYD. Dichotomous results applying the equal sensitivity and specificity threshold. The base map was created using ESRI ArcMap



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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.

178 In addition, habitat suitability was observed in Australia and Indonesia. The countries highly  
179 suitable for the disease in Africa stretches from the coastal regions of Senegal through Ghana to  
180 Angola. Other African countries found to be suitable for LYD in Africa were Kenya, Somalia,  
181 Djibouti, Tanzania and Eritrea. In the Southern America, the climate suitable areas included  
182 Brazil, Guyana, Venezuela, Suriname and French Guiana, whereas the coastal areas of India  
183 were suitable for the disease in South Asia. Our current prediction highlighted Bangladesh,  
184 Thailand and Burma as climate suitable areas for LYD, especially in the coastal regions. Overall,  
185 our projection exceeded the current distribution of the disease.  
186 The model forecasted more climate suitable areas for the crop outside its current range (Fig. 4).



187  
188 Figure 4: Modelled climatic suitability for *Cocos nucifera*. Based on GBIF occurrence data and  
189 four only little intercorrelated bioclim variables (bio15, bio04, bio06, and bio18) modelled on a  
190 global scale, MaxEnt model with LQP features only. The base map was created using ESRI  
191 ArcMap.  
192

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

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

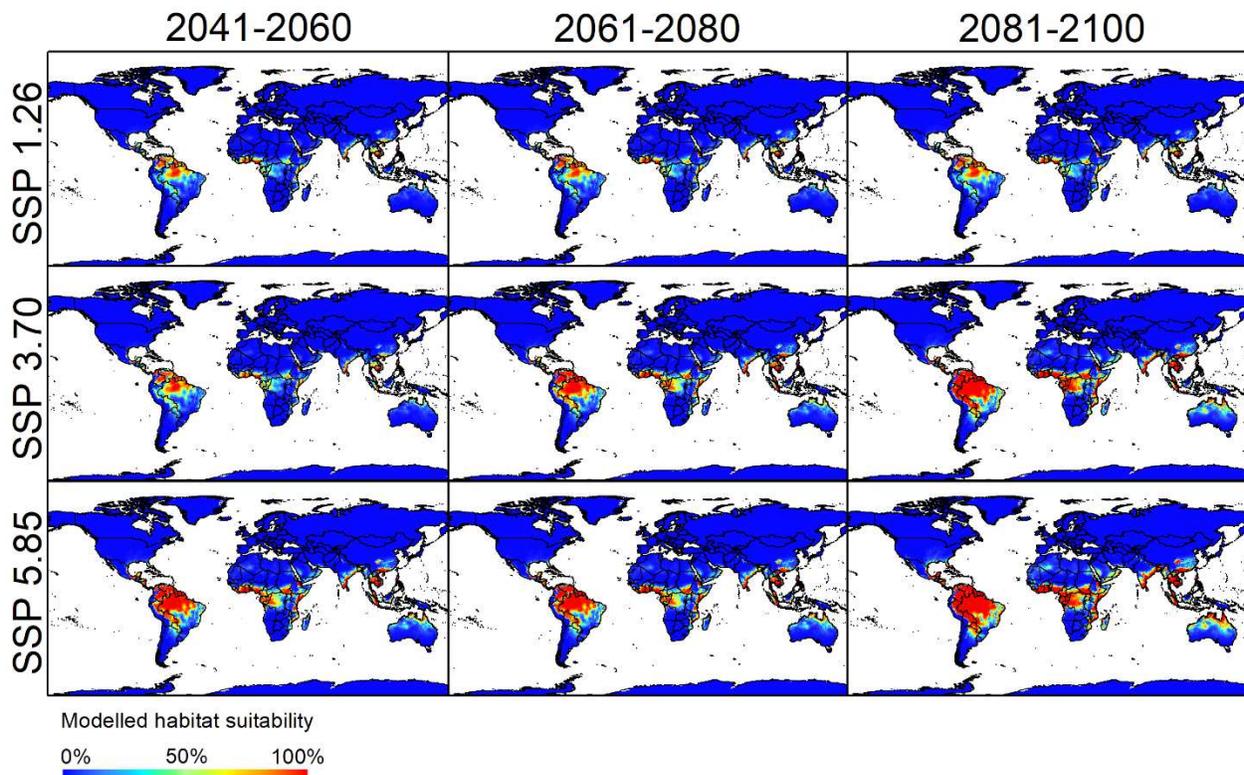
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### 202 **Projection of suitable areas of lethal yellowing-like diseases of coconut-future scenarios**

203

204 The MaxEnt model predicted LYD future distribution for three Shared Socio-economic Pathways  
205 (SSPs) (1.26, 3.70 and 5.85) (Fig. 5). A shift in LYD distribution from the current to future  
206 predictions was observed, as shown by the different hotspots in the affected areas. For the low  
207 climate change scenario (SSP1.26), there was no clear expansion of climate suitable areas of  
208 LYD from 2041-2060 to 2081-2100. The highly suitable areas of LYD in Africa stretches from  
209 Côte D'Ivoire through Ghana to Nigeria. The hotspots in South and South East Asia were along  
210 the coastal belts. However, in South America, there was an inland expansion of climate suitable  
211 areas of LYD, and the major areas at risk of spread were Brazil and the Guianas. Under the  
212 moderate climate change scenario (SSP3.70), there was consistent expansion of LYD suitable  
213 areas into new areas from 2041 to 2100. The highly suitable areas included South America,  
214 West Africa and Central Africa. The extreme scenario (SSP 5.85) showed an increase in potential  
215 climate-suitable areas of LYD from 2041-2060 to 2081-2100. Climate suitable areas that showed  
216 expansion of suitable areas were in the South America, Africa and Australia. However, most of  
217 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

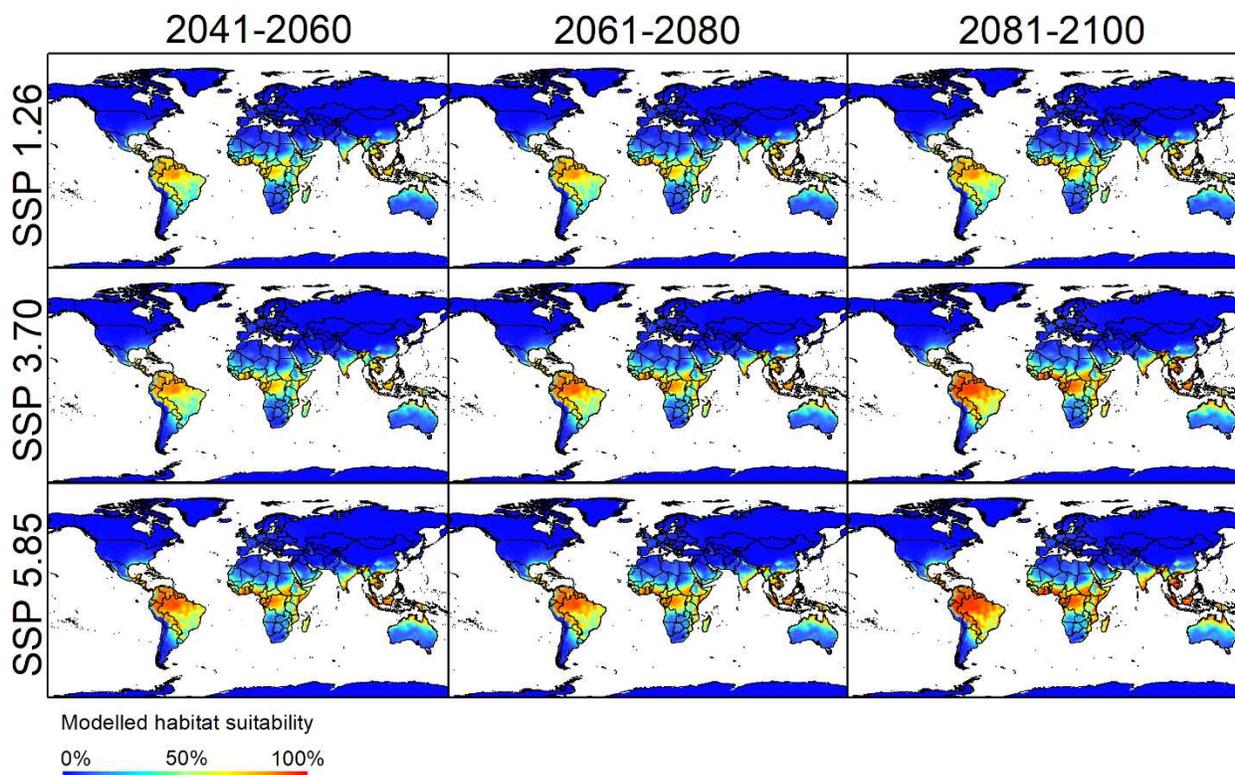
226

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

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



235  
236 Figure 6: Projected climatic suitability for *Cocos nucifera* under future climatic conditions. The  
237 base maps were created using ESRI ArcMap.  
238

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

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

250

## 251 **DISCUSSION**

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

265

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

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

289 Because the disease and the host plant overlapped in our projections, some countries in Africa  
290 (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<sup>43</sup>, America<sup>44</sup> and Asia<sup>45</sup>, 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<sup>46</sup> 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<sup>47</sup>. 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<sup>8</sup>. 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

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

316  
317 Several studies on putative vectors of LYD have been inconclusive because they failed to  
318 confirm the successful transmission of LYD from diseased-palms to healthy ones<sup>32,43</sup>. However,  
319 many insects have been implicated in the spread of the disease. For instance, the planthopper  
320 *Haplaxius crudus* Van Duzee, has been reported in Mexico<sup>49</sup>, *Nodoterpa curta* in Côte D'Ivoire<sup>50</sup>,  
321 *Platacantha lutea* Westwood and *Diostrombus mkurangai* Wilson in Mozambique and  
322 Tanzania<sup>41,51,52</sup> in Ghana<sup>53</sup>. The outbreak of LYD is marked with initial symptoms occurring in  
323 one or two palms followed by sporadic cases up to 100 m away from the primary infection,  
324 then further spread to few kilometers to about 100 km, which can be followed by a "jump" to  
325 anywhere<sup>43,54</sup>. The spread rate often appears to be irregular, with peaks occurring in a few  
326 months but not consistent in all coconut growing regions. Inconclusive results of vector  
327 identification coupled with the nature of disease spread, suggest that quarantine measures  
328 using output from our present study would help mitigate its spread to clean areas.

329  
330 Attempts to simulate LYD spread are difficult on a small scale<sup>54</sup>, but have been conducted on  
331 larger scales<sup>55</sup>. Geographic features such as mountain ranges, which may not allow vectors  
332 cross naturally, could affect the disease spread<sup>56</sup>. Anthropogenic activity appears to be a  
333 substantial cause of LYD spread through movement of plant materials and farm machinery. For  
334 example, grasses and palm trees imported from Florida to Mexico for new golf courses were

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

340

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

349

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

357 understand the ecology and possible risk of spreading this destructive disease through different  
358 coconut agroecosystems, all these factors need to be further investigated.  
359 High temperatures increase the rate of dispersal of certain phytoplasmas by faster  
360 multiplication in the host or higher feeding frequency of insect vectors, resulting in increased  
361 transmission possibilities<sup>64</sup>. Apart from temperature, climate change is closely linked with an  
362 increased occurrence of drought and storms that can increase plant stress<sup>65</sup>, exposing them to  
363 pests and disease attacks. Hurricanes could be associated with high incidence of LYD in the  
364 Caribbean.  
365 All presence-only data used for the MaxEnt model were obtained from secondary sources;  
366 except for Ghana. Therefore, the research corresponds to the definition advocated by the Open  
367 Science movement, which encourages data reuse for further exploration and decisions<sup>66</sup>.  
368 Models that only use presence-only data are easier to build and are common than those that  
369 jointly use input presence and absence data<sup>67</sup>. Presence data are usually easier to collect  
370 because confirming an organism's absence requires comprehensive and thorough surveys. Also,  
371 it may be difficult or costly to obtain such presence-absence data.

372

## 373 **CONCLUSION**

374 For the first time, we have established the suitable and unsuitable habitats of the most  
375 devastating coconut disease worldwide using bioclimatic variables. Our model performance  
376 was very good and reliable based on the current distribution of the disease in the four  
377 continents. The simulated LYD, would help to better understand the impact of climate change  
378 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<sup>59</sup>. 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 °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<sup>68</sup>.

395

### 396 **DNA Clean-up with PVPP**

397 To clean the DNA, we used a Micro-Bio-Spin column with chloroform-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

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

408

#### 409 **Conventional PCR**

410 For all polymerase chain reactions (PCR), 50–100 ng of sample DNA template was added to a  
411 25uL reaction. PCRs were carried out using MangoMix (Bioline, UK) containing: Mango Taq™  
412 polymerase, dNTPs, red and orange reference dyes and Mg<sup>2+</sup>. A forward and reverse primer at  
413 a final concentration of 0.2 μM was used in the reaction. For the detection of the LYD  
414 phytoplasma, the primers: CSPWDSecAFor2 / CSPWDSecARev2 <sup>69</sup> were used. The PCR cycling  
415 was as follows: one cycle at 94 °C for 3 min, followed by 35 cycles of 94 °C for 40 s, 55 °C for  
416 40s and 72 °C for 1 min 40s; and 1 cycle at 72 °C for 10 min. Five microliters of each of the PCR  
417 products were separated in a 1.5 % agarose gel and visualized with SYBR Safe DNA Gel Stain  
418 (Invitrogen, USA) in a UV transilluminator. Approximately 300bp fragments were obtained for  
419 positive tests.

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#### 423 **Collection of other LYD and coconut presence data**

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

441

#### 442 **Environmental data**

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

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

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469 Table 3. The bioclimatic variables that were considered in the MaxEnt model. Bold font  
 470 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
<b>Temperature seasonality (SD× 100)</b>	<b>°C</b>	<b>bio4</b>
Maximum temperature of warmest month	°C	bio5
<b>Minimum temperature of coldest month</b>	<b>°C</b>	<b>bio6</b>
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
<b>Precipitation seasonality</b>	<b>mm</b>	<b>bio15</b>
Precipitation of wettest quarter	mm	bio16
Precipitation of driest quarter	mm	bio17
<b>Precipitation of warmest quarter</b>	<b>mm</b>	<b>bio18</b>
Precipitation of coldest quarter	mm	bio19

471

472 The final environmental variables were minimum temperature of coldest month (bio6),  
 473 precipitation of warmest quarter (bio18), precipitation seasonality (bio15), and temperature  
 474 seasonality (bio4). For future projections, data according to the CNRM-ESM2-1 Global  
 475 Circulation model<sup>74</sup> for three Shared Socioeconomic Pathways (SSPs); 1.26, 3.70 and 5.85 and  
 476 three the time periods; 2041-2060, 2061-2080, 2081-2100. Global extent, spatial resolution of  
 477 2.5 arc minutes (~ 5\*5km<sup>2</sup>). All maps were created using ESRI ArcMap.

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479

## 480 **MaxEnt Model**

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

496

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## AUTHOR CONTRIBUTION

773 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.,  
774 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.  
775 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.  
776 wrote the paper; all authors revised the manuscript.

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## CONFLICT OF INTEREST

779 The authors declare no conflict of interest.

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783 **DATA AVAILABILITY STATEMENT**

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

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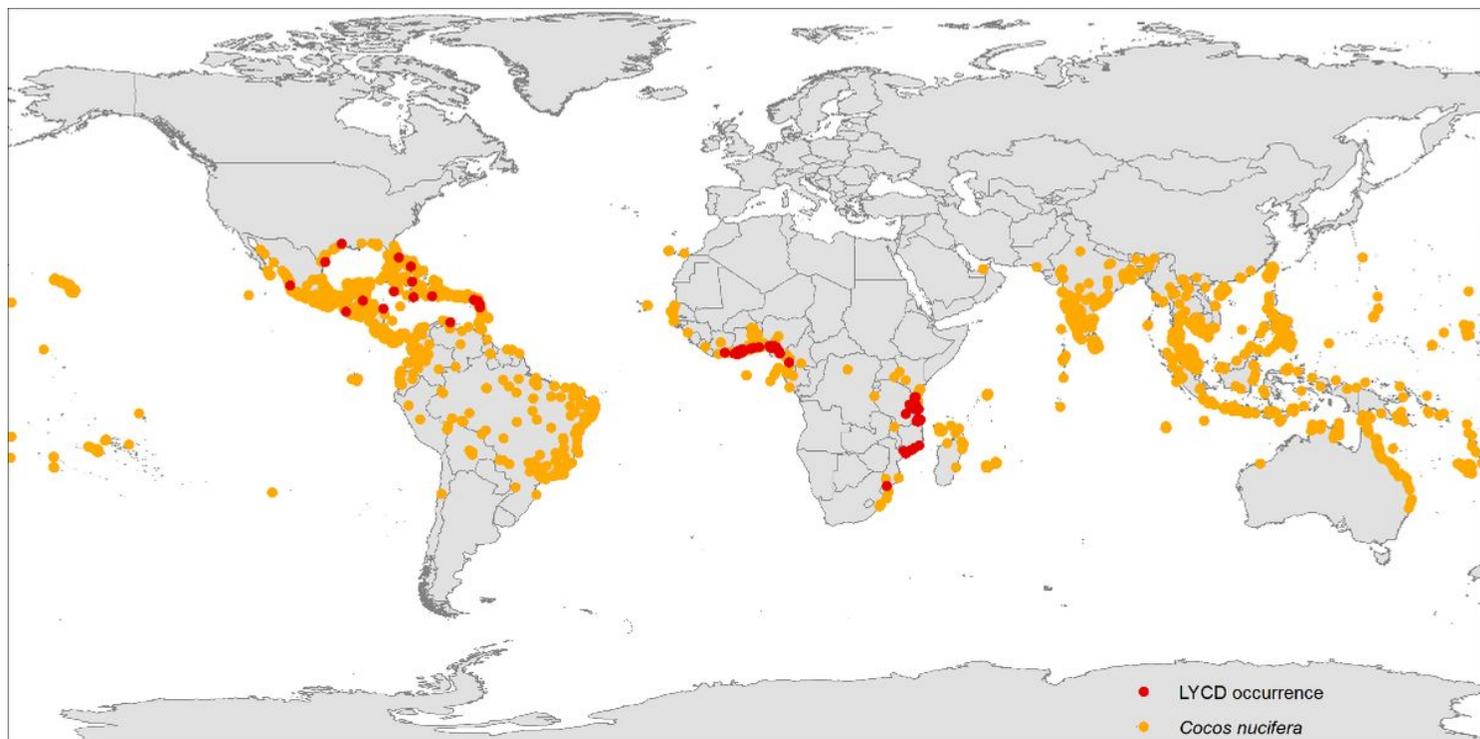
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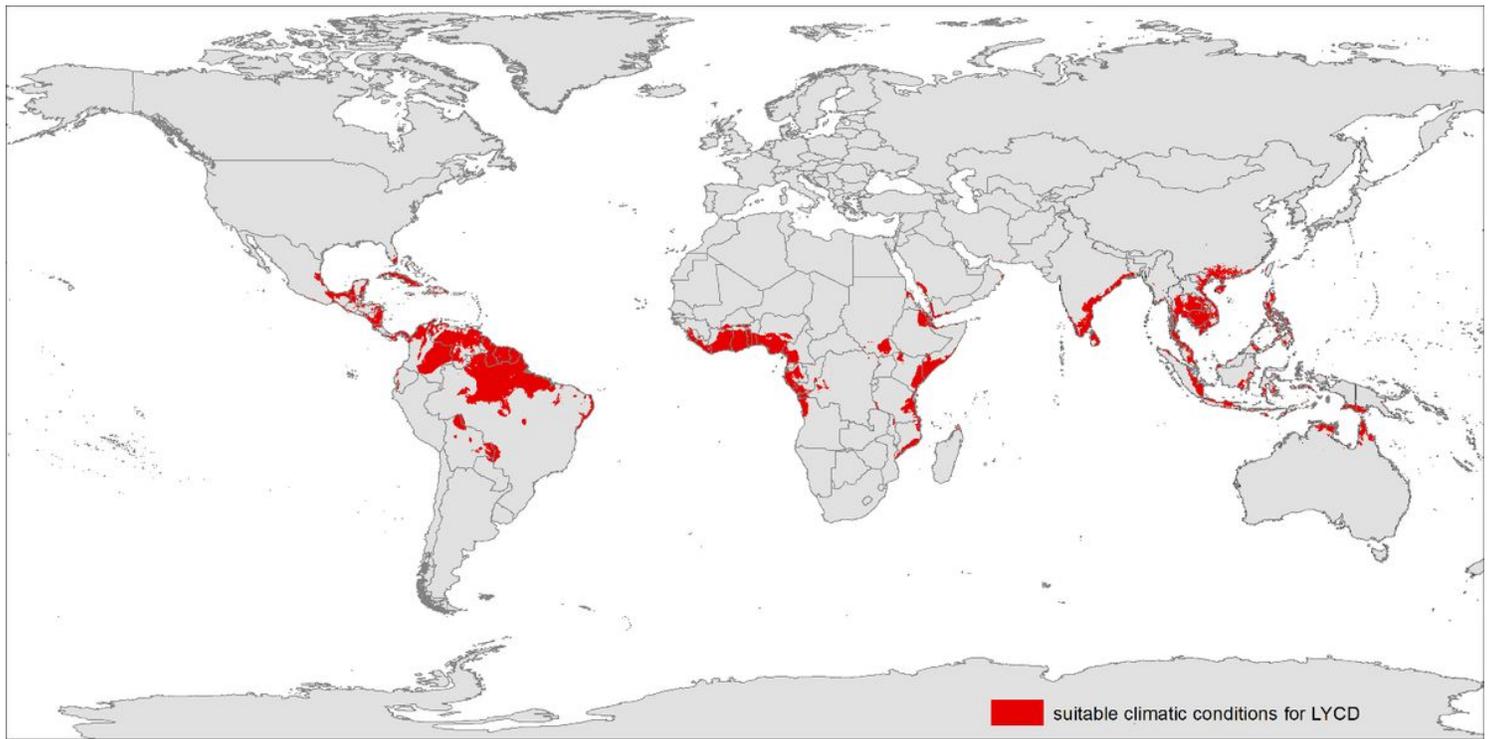
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## Figures



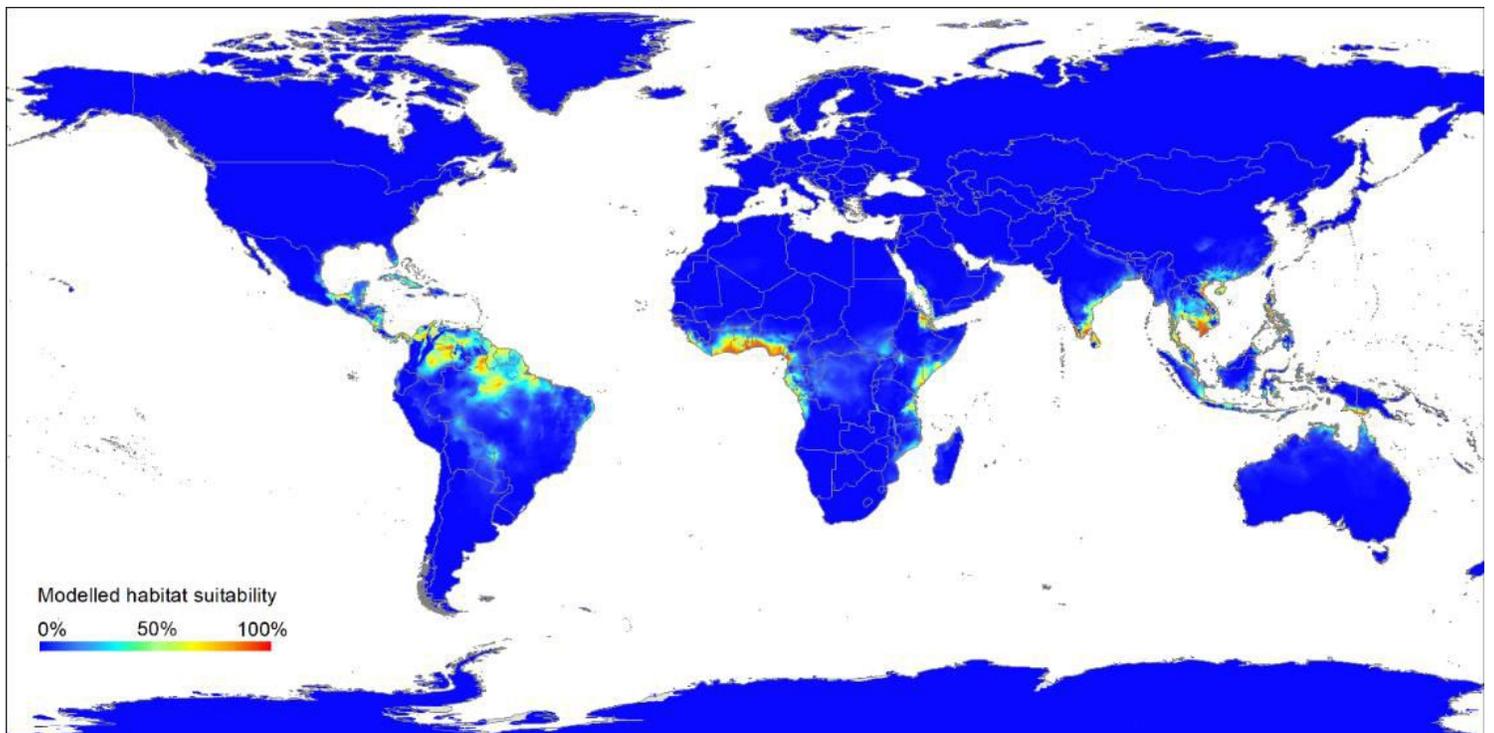
**Figure 1**

Occurrence data of LYD in comparison to GBIF occurrence records for *Cocos nucifera*. The base map was created using ESRI ArcMap. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



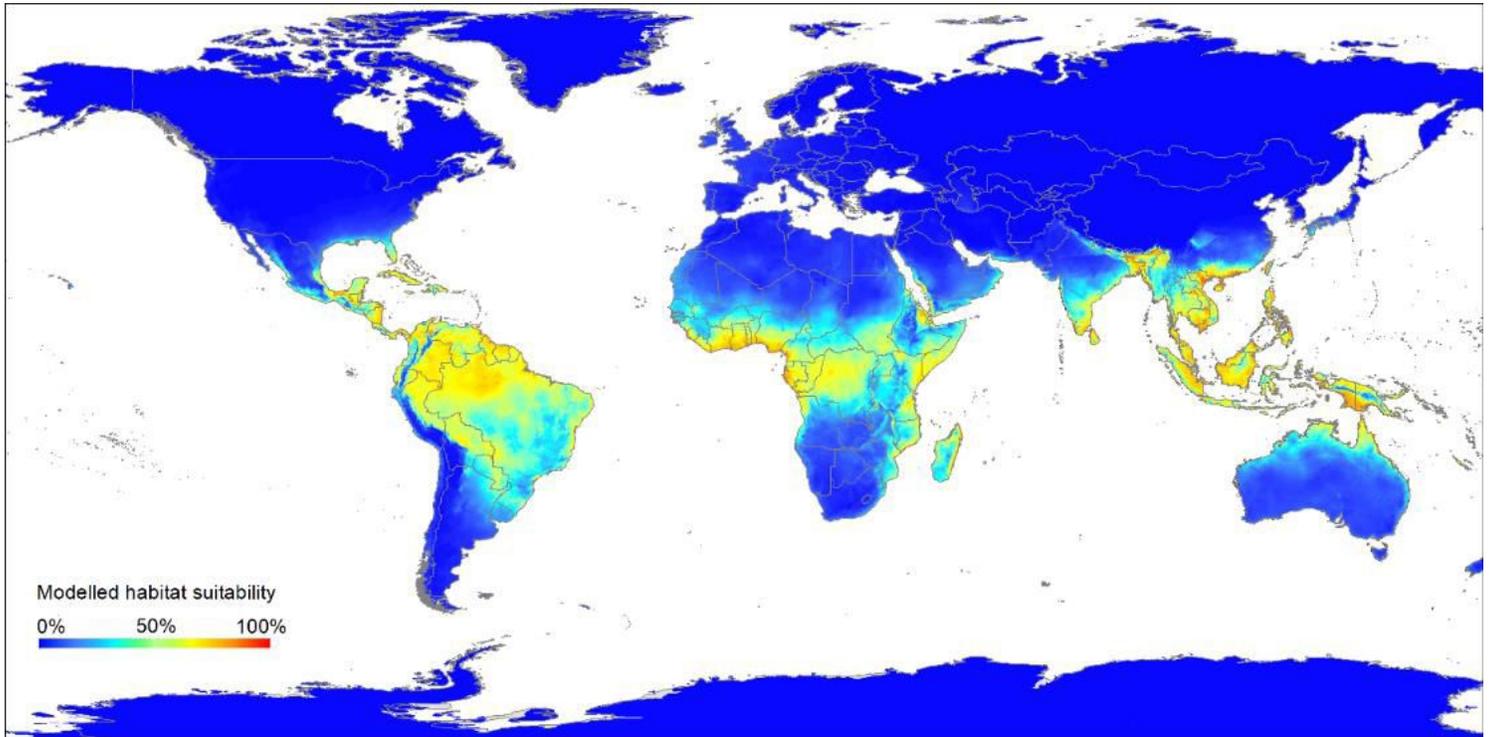
**Figure 2**

Area with modelled climatic suitability for LYD. Dichotomous results applying the equal sensitivity and specificity threshold. The base map was created using ESRI ArcMap Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



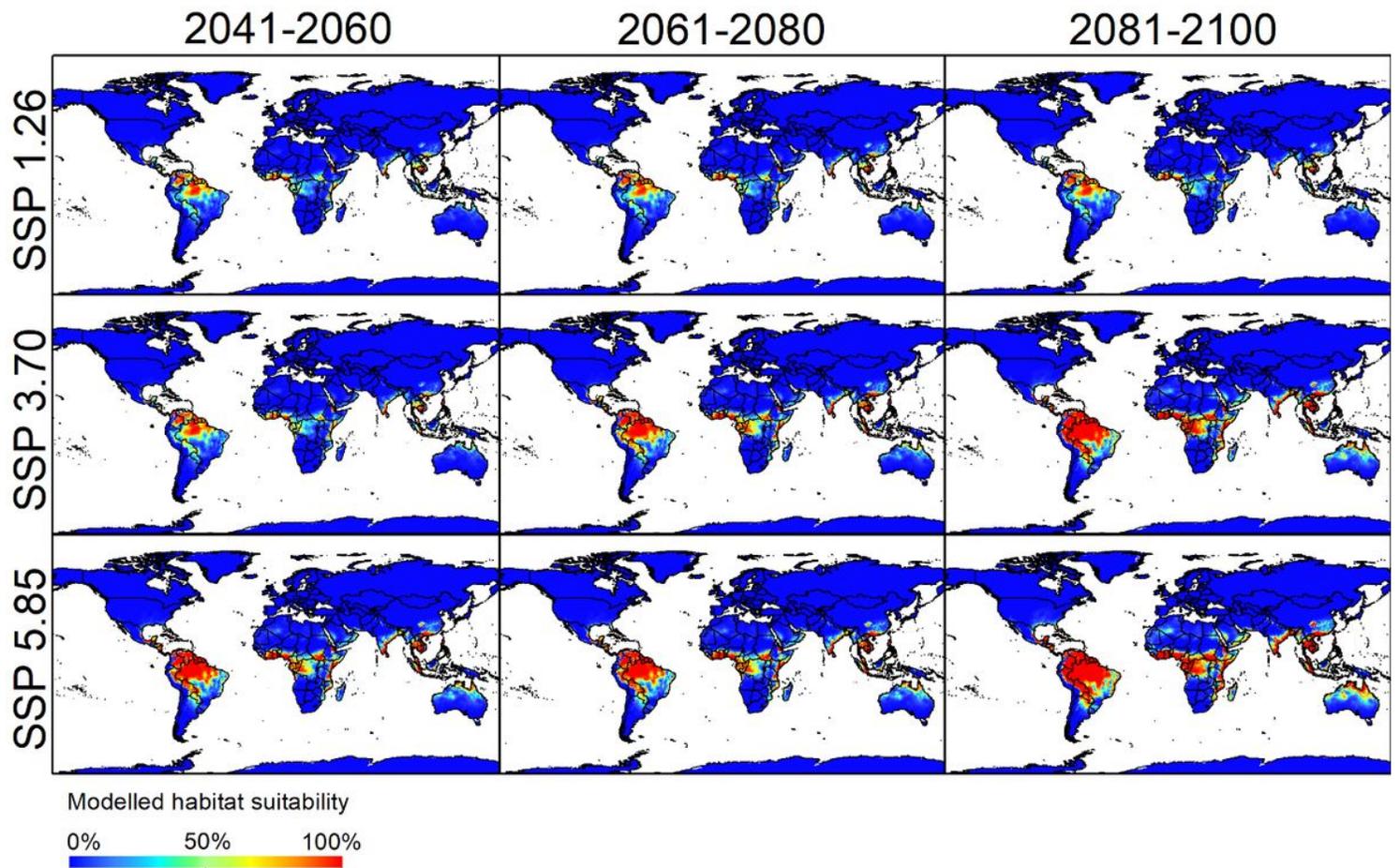
### Figure 3

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. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



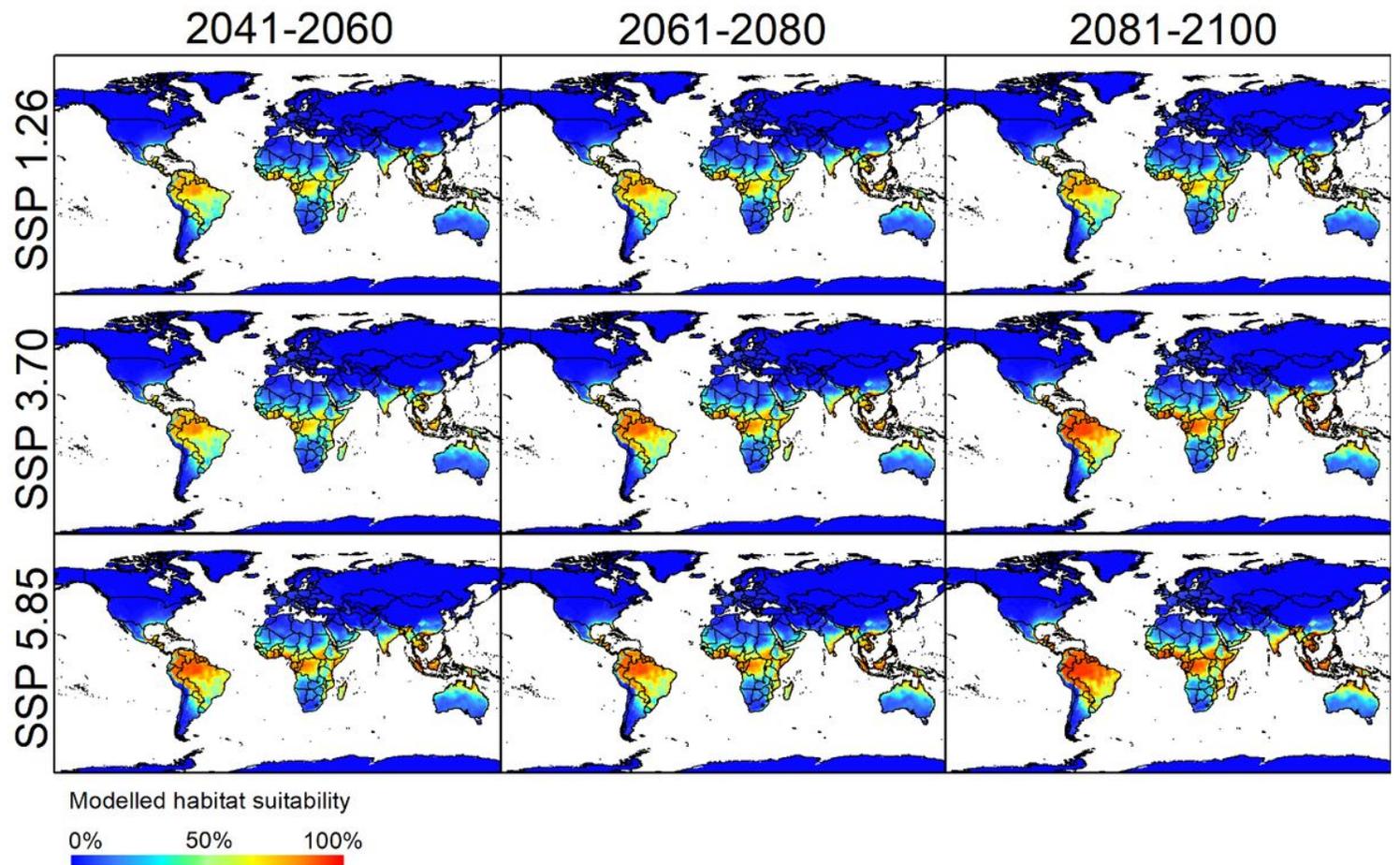
### Figure 4

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. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 5**

Projected climatic suitability for LYD under future climatic conditions. The base maps were created using ESRI ArcMap. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



**Figure 6**

Projected climatic suitability for *Cocos nucifera* under future climatic conditions. The base maps were created using ESRI ArcMap. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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