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The risk to Myrtaceae of *Austropuccinia psidii*, myrtle rust, in Mexico

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8 **Abstract**

9 *Austropuccinia psidii* is a biotrophic rust fungus that affects species from the Myrtaceae family.
10 In Mexico, Myrtaceae is widely distributed in temperate, tropical, and semi-arid ecosystems, and
11 includes 20 genera and 192 endemic and exotic species. *Austropuccinia psidii* has been present in
12 Mexico for the last four decades; however, little is known about the distribution of this rust or the
13 vulnerability of native and exotic Myrtaceae to infection. In this study, we used global occurrence
14 records for the pandemic biotype of myrtle rust to model its current and future suitable habitat
15 using a species distribution model, Maxent. We identified regions that are highly suitable for
16 myrtle rust establishment, now and in the future (2050). Additionally, we identified the
17 Myrtaceae species known to be susceptible to rust infection and that are currently distributed in
18 areas with high rust habitat suitability. Thirty-six susceptible plant species and 142 untested
19 species are distributed within areas of suitable rust habitat and are considered potentially at risk
20 of rust infection. Current suitable habitat is mainly restricted to the east coast of Mexico, with
21 Veracruz, Puebla, Chiapas, Tabasco, and Oaxaca being the most vulnerable regions to the rust
22 under current and future climates. We encourage monitoring within these regions by surveying
23 locations where the rust occurs and within areas with high suitable habitat to determine the threat
24 to native ecosystems and industries reliant on Myrtaceae. We also recommend screening to test
25 the susceptibility of Myrtaceae species with no known susceptibility rating.

26
27 **Key words:** fungi; habitat suitability; invasive species; Maxent; fungal pathogens; species
28 distribution model

29 1. INTRODUCTION

30 *Austropuccinia psidii* (formerly *Puccinia psidii*) (BEENKEN 2017) is known globally for its
31 devastating effects as an invasive pathogen of horticultural, agricultural and native species (GLEN
32 et al. 2007). This rust is native to Central and South America and was first reported in 1884 in
33 Brazil (COUTINHO et al. 1998; GLEN et al. 2007; WINTER 1884). Outside of its native distribution,
34 the rust can be found in Australia, China, Costa Rica, Indonesia, Jamaica, Japan, Mexico, New
35 Caledonia, Puerto Rico, Singapore, South Africa, U.S.A. (Florida and Hawaii), and most recently
36 Colombia and New Zealand (CARNEGIE et al. 2010; DU PLESSIS et al. 2017; GIBLIN 2013;
37 KAWANISHI et al. 2009; MARLATT; KIMBROUGH 1980; MCTAGGART et al. 2016; MPI 2017;
38 ROUX et al. 2013; UCHIDA et al. 2006; ZHUANG; WEI 2011). The population structure and host
39 specificity of the rust vary according to its distribution. While multiple biotypes have been
40 identified via molecular analysis (GRAÇA et al. 2011), the pandemic biotype occurs in Australia,
41 Costa Rica, Indonesia, Jamaica, Mexico, New Caledonia, Puerto Rico, Hawaii, and has recently
42 been found in Colombia (GRANADOS et al. 2017; MACHADO et al. 2015; STEWART et al. 2017).

43 The pandemic biotype of *A. psidii* represents a threat for local biodiversity because of its
44 rapid dissemination, wide host range and the severe damage reported for some species (BERTHON
45 et al. 2018; CARNEGIE et al. 2016; LOOPE 2010; PEGG et al. 2017; UCHIDA; LOOPE 2009). Lesions
46 caused by the fungus mainly appear on young, growing leaves and shoots, but also on flowers
47 and fruits. During early stages of infection, chlorotic flecks on leaves and shoots can be observed,
48 followed by the production of masses of bright yellow urediniospores (PEGG et al. 2014; SIMPSON
49 et al. 2006; WALKER 1983). In later stages of infection, the impact on individual trees and shrubs
50 range from minor leaf spots through to reduced fecundity from loss of flowers and fruit, and even
51 tree mortality (PEGG et al. 2014).

52 *Austropuccinia psidii* affects species from the Myrtaceae family (BOOTH et al. 2000).
53 While genera and species within Myrtaceae vary in their susceptibility to this rust (BOOTH et al.
54 2000), it is considered a serious threat to *Eucalyptus* species (CARNEGIE; COOPER 2011;
55 COUTINHO et al. 1998; DIANESE et al. 1984; FERREIRA 1983) and has caused extirpation of native
56 species in ecosystems in Australia (CARNEGIE et al. 2016). In Mexico, Myrtaceae is widely
57 distributed in temperate, tropical, and semi-arid regions (MONROY-ORTÍZ; MONROY 2006), with
58 approximately 20 genera and 192 species—including 30 *Eucalyptus* species—distributed across
59 the country (Global Biodiversity Information Facility, GBIF; www.gbif.org). The family is
60 recognized for its economic and cultural importance, providing timber, fruits, spices and

61 condiments, essential oils and nectar, and also for its medicinal and ornamental value, among
62 others (ARELLANO RODRÍGUEZ et al. 2003; CABRERA et al. 2001; MONROY-ORTÍZ; MONROY
63 2006; TERÁN; RASMUSSEN 1994).

64 In Mexico, the negative impact of other rust fungi on natural environments and crops has
65 been documented. Examples include the invasion of coffee rust (*Hemileia vastratix*) (LÓPEZ
66 RAMÍREZ 1998; LÓPEZ RAMÍREZ; CELIS 1982); *Gymnosporangium clavipes*, which infests species
67 of the genus *Crataegus* (commonly called ‘tejocote’) (ALVARADO-ROSALES et al. 2015); and
68 *Cronartium ribicola*, which causes white pine blister rust (LÓPEZ-PERALTA; SANCHEZ-CABRERA
69 1996). Indeed, it is estimated that there are at least 651 rust species associated with 13 plant
70 families in Mexico, but rusts specific to Myrtaceae is not included in this estimate (BERNDT
71 2012; FARR; ROSSMAN 2011; VILLASEÑOR 2003).

72 Presently, there is a paucity of published information on myrtle rust in Mexico. The
73 pathogen has been known in the country for four decades. However, there are only eight rust
74 specimens for the country (from Veracruz and Chiapas) deposited in herbaria (RAMÍREZ
75 GUILLÉN PERS. COMM., 2017; ROSS-DAVIES PERS. COMM., 2016; GBIF). These collections
76 were made from regions characterised by high altitude and precipitation. *Pimienta* (hereafter
77 *Pim.*) *dioica* is reported as its first host (LEÓN GALLEGOS; CUMMINS 1981), but the rust has also
78 caused damage to *Syzygium jambos*, leading to environmental and economic impacts (LEÓN
79 GALLEGOS; CUMMINS 1981; LOPEZ; GARCÍA 2011; STEWART et al. 2017).

80 The economic, ecological and cultural importance of Myrtaceae in Mexico means that
81 myrtle rust may have serious consequences to both native ecosystems and commercial industries,
82 although the magnitude of potential impacts remains unknown. Additionally, the lack of studies
83 related to host susceptibility and rust occurrence makes it difficult to estimate the rust’s potential
84 distribution and to identify the host species most vulnerable to damage. The aims of our study
85 were to determine suitable habitat for myrtle rust in Mexico under current and future climates
86 with climatic modelling and to identify Myrtaceae species present in Mexico that are known to be
87 susceptible to infection and likely to be highly exposed to this rust.

88

89 **2. METHODS**

90 **2.1. Occurrence records data**

91 We undertook an exhaustive search to compile global occurrence data for *A. psidii* from a variety
92 of sources. Specifically, we sought records from countries that have the same biotype of myrtle

93 rust as Mexico, the pandemic biotype (MACHADO et al. 2015; STEWART et al. 2017), which
94 include Australia, Costa Rica, Indonesia, Jamaica, Puerto Rico, and Hawaii (U.S.A.). For records
95 in Mexico, we searched data from GBIF, the Biological Collections of the National Autonomous
96 University of Mexico (UNIBIO), the National Commission for the Knowledge and Use of
97 Biodiversity (CONABIO), the Global Biodiversity Information (REMIB), literature, and via
98 personal communications (see acknowledgments). For records outside Mexico, the sources used
99 included databases from the Australian Government (New South Wales, Queensland, Tasmania,
100 Victoria and Northern Territory government departments), recent literature (MACHADO et al.
101 2015; MCTAGGART et al. 2016; POTTS et al. 2016), validated sightings from Australia's Myrtle
102 Rust Environmental Impacts Working Group, and via personal communications. We collected a
103 total of 2385 Australian records and 50 records of natural infection outside of Australia.

104 Occurrence records were cleaned by removing those that contained missing or incorrect
105 coordinates, or where the location could not be identified. The source of infection varied across
106 records and was classified as nurseries, gardens, and natural environments. For model
107 development, we used only those records corresponding to natural environments because these
108 records reflect the natural conditions in which the rust grows, as per BERTHON et al. (2018).

109 **2.2. Modelling habitat suitability**

110 We used Maxent version 3.4.1 (PHILLIPS et al. 2017) to model climatic suitability for the
111 pandemic biotype of myrtle rust. Maxent is a commonly used machine learning approach to
112 modelling habitat suitability, favoured due to its high performance (ELITH et al. 2006). This
113 model produces a relative index of suitability ranging from 0 to 1. Areas with higher values are
114 hypothesised to have greater suitability for the modelled species (PHILLIPS; DUDIK 2008;
115 PHILLIPS et al. 2006).

116 We downloaded data for 19 climatic variables (**Supplemental Table S1**) from
117 WorldClim version 1.4 (HIJMANS et al. 2005), at a resolution of 30 arc-seconds (~1 km) for
118 model calibration. Data were projected using EPSG:4326 (longitude/latitude WGS84). We
119 considered these data, which describe conditions for the period 1960–1990, to reflect the baseline
120 (or current) climate. To select variables for model calibration, we evaluated correlations among
121 climatic variables using Pearson correlation (LEGENDRE; LEGENDRE 2012) identifying pairwise
122 combinations of variables with a correlation coefficient ≤ 0.7 . We then selected three subsets of
123 variables for model calibration based on trade-offs between biological significance and
124 multicollinearity constraints. Of these, we selected the set that produced a climate suitability map

125 most consistent with previous work and expert opinion. We then assessed the response curves
126 and permutation importance generated by Maxent, and selected a final set of five variables
127 consisting of temperature seasonality (TS), maximum temperature of the warmest month
128 (TmaxWM), annual precipitation (AP), precipitation of the wettest month (PWM), and
129 precipitation seasonality (PS).

130 Of the occurrence records of the pandemic biotype, 701 were collected from natural
131 environments around the world, 651 of which were from Australia. After accounting for multiple
132 records in a single grid cell, we used 276 unique locations (at a resolution of 1 x 1 km) to fit our
133 model. The general background of environmental conditions was represented by a sample of
134 100,000 points randomly selected from within 200 km of occurrence records. We modified the
135 Maxent default settings to improve model performance (SYFERT et al. 2013), disabling hinge and
136 threshold features to avoid locally overfit response curves.

137 We estimated model performance by calculating the average test AUC (Area Under the
138 Receiver Operating Characteristic curve, SWETS 1988) derived from five-fold cross-validation.
139 This approach entailed splitting occurrence and background data into five subsets (i.e., folds),
140 fitting the model to four folds and predicting to the fifth. We repeated this process such that each
141 fold was used four times for model fitting and once for model evaluation (STONE 1974). The
142 model was then fit a final time using the complete set of myrtle rust occurrence data (i.e., 276
143 records). This model was used for subsequent analyses.

144 Due to the limited occurrence data of the pandemic biotype outside of Australia, we
145 acknowledge that the estimated niche for myrtle rust might presumably be biased to Australian
146 environmental conditions. Thus, we visually assessed our model by projecting it and developing
147 maps of suitable habitat for each country with occurrence data available: Australia, Costa Rica,
148 Indonesia, Jamaica, Puerto Rico, Hawaii (U.S.A.), and New Caledonia (**Supplemental Figure**
149 **S1**).

150 To assess future climate suitability, we downloaded data from WorldClim for the time
151 period 2050 (average for 2041-2060) at a resolution of 30 arc-seconds (~1 km) (EPSG:4326;
152 longitude/latitude WGS84) (HIJMANS et al. 2005). We used scenarios from 17 global circulation
153 models (GCMs) (**Supplemental Table S2**) and for the Representative Concentration Pathway
154 (RCP) 8.5. RCPs are consistent with a wide range of possible changes in future anthropogenic
155 greenhouse gas emissions. For RCP 8.5, emissions continue to rise throughout the 21st century
156 (MEINSHAUSEN et al. 2011). We projected climate suitability for myrtle rust onto each of the 17

157 scenarios and calculated the average and standard deviation of these projections. We followed
158 this approach due to the variation among different GCMs in terms of projected temperature and
159 precipitation trends. Thus, our models represent a broad range of projected variation in future
160 conditions. Additionally, we developed an agreement map across all 17 GCMs. This map
161 highlights areas projected to have high habitat suitability across all possible future climates until
162 at least 2050. For this approach, we converted the continuous suitability predictions to binary
163 layers indicating suitable/unsuitable habitat. We used as threshold the 10th percentile for training
164 presence/training omission (for our model, 0.0978), which assumes that 10% of the training (or
165 test) occurrences are predicted as unsuitable (PHILLIPS et al. 2004). We acknowledge that this
166 threshold might over-estimate habitat suitability, but because myrtle rust is an invasive species
167 we consider this approach more valuable.

168 We developed Multivariate Environmental Similarity Surface (MESS) maps to assess the
169 projection to new climates. These maps allowed us to identify those areas where projections were
170 extrapolated (ELITH et al. 2010). All modelling and calculation of statistics were performed in R
171 version 3.1.2 (R CORE TEAM 2016), using customised code based on ‘dismo’ (HIJMANS et al.
172 2016) to fit Maxent models, with additional code from ‘rmaxent’ (BAUMGARTNER et al. 2017).

173

174 2.3. Myrtaceae species at potential risk of myrtle rust infection in Mexico

175 We queried the Global Biodiversity Information Facility (GBIF, <http://www.gbif.org>) to identify
176 all Myrtaceae species occurring in Mexico. Occurrence records were filtered to remove non-
177 georeferenced records, as well as those observed prior to 1950. We kept records with no known
178 coordinates issues, and for which the basis of observation was reported as “human observation”,
179 “observation”, “specimen”, “living specimen”, “literature occurrence”, and “material sample”.
180 Then, we identify species whose occurrence records were contained within areas projected to be
181 suitable for myrtle rust, and based on previous studies (see references in **Table 1**), identified
182 species known to be susceptible to rust infection.

183

184 3. RESULTS

185 We found eight records of myrtle rust from four unique locations in Mexico. One record was
186 located at Ocozocoautla, Chiapas (RAMÍREZ GUILLÉN PERS. COMM., 2017), and seven records
187 in Veracruz, South of Xalapa (GBIF; ROSS-DAVIES PERS. COMM., 2016) (**Supplemental Table**
188 **S3**). Records from Veracruz fell within our predicted suitable habitat (**Figure 1**). We obtained an

189 AUC value of 0.934 for our final model (see full output model in **Appendix 1**), which indicates
190 high classifier performance (SWETS 1988). Of the five variables, annual precipitation had the
191 highest permutation importance, while maximum temperature of the warmest month had the
192 lowest (**Table 1**). MESS maps indicated that regions projected to be climatically suitable for
193 myrtle rust under current and future conditions do not contain novel climates (**Supplemental**
194 **Figure S2**). This finding increases the confidence we can place in projections of suitable habitat.

195 Our findings of suitable habitat for myrtle rust are consistent with previous work (BOOTH
196 et al. 2000; ROSS-DAVIS et al. 2013; STEWART et al. 2017). Our model fits closely to the
197 distribution of the pandemic biotype of myrtle rust in Hawaii (ANDERSON 2012) and New
198 Caledonia (SOEWARTO et al. 2017), both of which have extensive occurrence records. However,
199 there are currently too few published occurrence records for Jamaica, Costa Rica, Puerto Rico,
200 and Indonesia to gauge the model's accuracy for these countries (**Supplemental Figure S1**).

201 **3.1. Suitable habitat for myrtle rust**

202 We estimated current suitable habitat for the pandemic biotype of myrtle rust in Mexico to span
203 an area of 318,442 km². Areas that are currently most suitable for the rust are mainly restricted to
204 the east coast of Mexico and include regions from Nuevo Leon, Tamaulipas, Veracruz, east of
205 San Luis Potosi, north of Puebla and Hidalgo, Oaxaca, Tabasco, Chiapas, south of Campeche,
206 Quintana Roo, and Yucatan. From these states, the highest suitability is projected in Veracruz,
207 Puebla, Chiapas, Tabasco, and Oaxaca. On the west coast, areas of higher vulnerability are
208 predicted in the west of Durango, south of Sinaloa, Nayarit, Jalisco, Michoacan, Mexico, and
209 Guerrero (**Figure 1 and Supplemental Figure S3**).

210 An area of 334,798 km² of future suitable habitat was predicted under at least one of the
211 17 climate scenarios. This result represents an increase of ~ 5% in the area projected to contain
212 suitable habitat for the rust, mainly in Veracruz, Puebla, Chiapas, Tabasco, and Oaxaca by 2050.
213 Conversely, suitable areas in the Yucatan Peninsula are predicted to decrease by 2050. Regions in
214 Tamaulipas, Nuevo León, Jalisco, and central Mexico are predicted to maintain similar areas of
215 suitable rust habitat at least until 2050 (**Figure 2**). Importantly, regions from Veracruz, north of
216 Puebla, Oaxaca, Chiapas, and Tabasco are predicted to remain suitable until at least 2050 across
217 all climate scenarios used in this study. For other regions in central and west Mexico, suitable
218 habitat was projected under at least ten climate scenarios (**Figure 3**).

219 **3.2. Myrtaceae species at potential risk of myrtle rust infection in Mexico**

220 According to GBIF data, there are 192 Myrtaceae species in Mexico. Of these, 36 species —
221 including 13 *Eucalyptus* species— have been previously tested for rust susceptibility, and only
222 three of these species are native to Mexico — *Pim. dioica*, *Psidium* (hereafter *Psid.*) *guajava*, and
223 *Syzygium megacarpum*. Ten species have a high proportion of their occurrence records
224 overlapping areas of high suitability for myrtle rust under current and future climates: *Melaleuca*
225 *citrinus* (syn. *Callistemon citrina*), *M. salignus* (syn. *C. salicina*), *Eucalyptus* (hereafter *Euc.*)
226 *camaldulensis*, *Euc. cinerea*, *Euc. gunnii*, *Eugenia* (hereafter *Eug.*) *uniflora*, *Pim. dioica*, *Psid.*
227 *cattleianum*, *S. malaccense*, and *S. megacarpum* (**Table 2**).

228 Additionally, another 142 species —including 17 *Eucalyptus* species— are distributed in
229 areas containing suitable habitat for myrtle rust but have not yet been tested for susceptibility. Of
230 these species, 39 are introduced and 103 are native. Four of these native species (*Eug. colipensis*,
231 *Eug. mozomboensis*, *Eug. salamensis*, and *Eug. uxpanapensis*) are listed as
232 endangered/vulnerable (IUCN 2017). *Calyptanthes pallens*, *C. schiedeana*, *Eug. capuli*, *Eug.*
233 *oerstediana* and *Myrcianthes fragrans* are the most widespread species occurring throughout
234 areas containing suitable habitat for the rust (**Supplemental Figure S3; Supplemental Table**
235 **S4**).

236 Of the high-risk states, Chiapas, Veracruz, and Oaxaca have the highest number of
237 Myrtaceae species (93, 75, and 44 respectively) (**Table 2 and Supplemental Table S4**) and the
238 greatest extent of current and predicted future suitable habitat for the rust (**Figures 1 and 2**). For
239 these states, the exotic *M. citrinus*, *Euc. camaldulensis*, *Euc. globulus*, *Euc. gunnii*, *Euc.*
240 *tereticornis*, *S. jambos*, and the native *Pim. dioica* are known to be susceptible to rust infection
241 (MORIN et al. 2012; PEGG et al. 2014; POTTS et al. 2016; SANDHU; PARK 2013). Conversely,
242 Durango and Michoacan have the lowest numbers of Myrtaceae species, with one and two
243 species respectively (**Table 2 and Supplemental Table S4**).

244

245 4. DISCUSSION

246 The east coast of Mexico is predicted to have the greatest expanse of suitable habitat for myrtle
247 rust under current and future scenarios, with Veracruz and Chiapas being the most vulnerable
248 states. This finding is consistent with the known presence of the rust in Mexico, as the only
249 records reported for the rust are in these states. We found 36 Myrtaceae species known to be
250 susceptible to rust infection distributed in areas that have high habitat suitability for the rust.
251 Hence, we consider species such *Pim. dioica*, *S. jambos*, and *M. citrinus* to be highly vulnerable

252 to myrtle rust. We also found 142 species with unknown susceptibility distributed within the
253 rust's suitable habitat. Our findings highlight the potential risk to native ecosystems and
254 commercial industries from the rust pandemic. Surveys are essential to monitor the spread of the
255 disease in Mexico and to find the true extent of the host range.

256 4.1. Suitable habitat for myrtle rust

257 Only eight rust collections of *A. psidii* from Mexico have been lodged in herbaria. This finding
258 highlights the need to improve the occurrence data for the country. Records are located at
259 Ocozocoautla, Chiapas, and Veracruz, South of Xalapa, within the Region of the Great
260 Mountains (RGM). Both locations in Chiapas and Veracruz are characterised by their steep
261 elevation gradients and high precipitation. Annual precipitation in RGM ranges from 600 to 1200
262 mm, with a maximum of 3000 mm in the wetter regions, whereas annual precipitation in
263 Ocozocoautla ranges from 420 to 950 mm, with a maximum of 1770 mm. The temperature in
264 these regions ranges from 10 to 29 °C in Veracruz, and 19 to 26 °C in Chiapas (BARRADAS et al.
265 2010; INEGI 2003). Previous work has shown that myrtle rust presence is associated with areas
266 of temperate temperatures, and high precipitation and elevation (BOOTH et al. 2000; GRANADOS
267 et al. 2017). We found precipitation to be the most important variable delimiting the presence of
268 suitable habitat for the rust (Table 1).

269 Future changes in precipitation and temperature will alter the distribution of suitable
270 habitat for myrtle rust. The increase in suitability in Veracruz may be driven by the predicted
271 increase of precipitation and cooler temperatures in some regions (ESPERÓN-RODRÍGUEZ et al.
272 2016). Conversely, the projected decrease in future suitable habitat in the Yucatan Peninsula may
273 be driven by predicted declines in precipitation (SWAIN; HAYHOE 2015). However, simulations
274 show that some drier regions of Mexico (precipitation below 450 mm) may be vulnerable to rust
275 invasion provided temperatures are not too high (BOOTH et al. 2000). Because temperature affects
276 the life cycle of the rust during different spore stages (FIQUEIREDO et al. 1984; PIZA; RIBEIRO
277 1989; RUIZ et al. 1987), more research is needed to understand how a future warmer climate
278 might affect infection and germination rates and how different spore types might be favoured by
279 warmer conditions.

280 It is also possible that a different biotype of myrtle rust, with a different climatic niche,
281 may be introduced to Mexico (STEWART et al. 2017). For example, other biotypes of myrtle rust
282 are known to severely impact eucalypt plantations in Brazil (FERREIRA 1983). Similarly, *A. psidii*
283 had been known from Jamaica for some years prior to the introduction of a new biotype that

284 caused severe disease in allspice (*Pim. dioica*) plantations in the 1930s (MACLACHLAN 1938). If
285 the rust extends its distribution, or a new biotype is introduced into Mexico via commercial ports,
286 Myrtaceae species may be severely affected. For future climate, areas with suitable habitat for the
287 rust in Veracruz and Nayarit might be particularly vulnerable due to their commercial activities.

288
289

290 **4.2. Myrtaceae species at potential risk of myrtle rust infection in Mexico**

291 We found 36 species of Myrtaceae—including endemic species and species of commercial
292 importance—potentially threatened by the pandemic biotype of myrtle rust based on our model
293 of suitable habitat for the rust and overlap with species' distributions. We consider *Pim. dioica*
294 and *S. jambos* as the most vulnerable species to myrtle rust in Mexico. Both species are known to
295 host *A. psidii* (LEÓN GALLEGOS; CUMMINS 1981; LOPEZ; GARCÍA 2011; PEGG et al. 2014; SANDHU;
296 PARK 2013; STEWART et al. 2017), are reported to be severely affected by the rust (CARNEGIE;
297 COOPER 2011; LEÓN GALLEGOS; CUMMINS 1981; MACLACHLAN 1938; MORIN et al. 2012; RAO
298 et al. 2012; UCHIDA; LOOPE 2009), a high proportion of their distributions overlaps areas with
299 high rust suitability, and have economic value, cultural and environmental importance (BEGOSI
300 et al. 2002; LIOGIER; MARTORELL 2000; SOTO-PINTO et al. 2007).

301 Other species, such as *M. citrinus*, *M. rigidus*, and *M. salignus* are also susceptible to
302 myrtle rust (MORIN et al. 2012; PEGG et al. 2014; SANDHU; PARK 2013) and are used in
303 cultivation, landscaping, and gardening throughout Mexico. Given that a high number of rust
304 occurrence records in Australia were reported from gardens, we highlight the value of monitoring
305 the Myrtaceae species in Mexican gardens, particularly of species known to be susceptible to the
306 rust (**Table 2**).

307 Presently, it is difficult to account for the potential risk myrtle rust poses to members of
308 the Myrtaceae family in Mexico, as few species in the country (19%) have been tested for
309 susceptibility (**Tables 2 and Supplemental Table S4**). Testing species susceptibility was beyond
310 the scope of this study, but we highlight that the presence of 142 non-tested species—including
311 species listed as endangered or vulnerable (IUCN 2017)—throughout areas with high rust habitat
312 suitability represent a potential risk. For these species, we recommend field surveys and
313 screening to determine their susceptibility to myrtle rust. In regards to the *Eucalyptus* species,
314 Mexico has an estimated of eleven million hectares of eucalypt plantations (RUIZ et al. 2006).
315 There are 30 *Eucalyptus* species in areas containing current and future suitable habitat for the

316 rust, but at present, only 13 have been screened for rust susceptibility (**Table 2**). Without
317 assessing susceptibility via inoculations, the risk to these species remains unclear. Future research
318 should be directed to test whether these species could host myrtle rust.

319 **4.3. What are the limitations of our study?**

320 We acknowledge some extrinsic limitations of our study. These include uncertainty in future
321 climate scenarios, host range susceptibility across all Myrtaceae species, our understanding of
322 current and potential changes in the genetics of the pathogen, and the impact that repeated year to
323 year moderate infections may have on the responses of hosts. Future research might be directed
324 to model the potential distribution of the host species under climate change, and assess
325 overlapping areas of current and future suitable habitat for both pathogen and host. However, this
326 step will require a rigorous collection of occurrence data for Myrtaceae in Mexico, which to date
327 has been challenging.

328 We also point out that our model is only suitable for the pandemic biotype of myrtle rust,
329 and included a limited number of occurrence records in Mexico. If additional observations are
330 uncovered during surveys, recalibrating models will help to develop more rigorous projections of
331 suitable habitat. This is particularly relevant if a new biotype is found, considering that different
332 biotypes have different climatic preferences (ELITH et al. 2013). Nonetheless, we reiterate that
333 our model projection is mostly consistent with previous work modelling the rusts' global
334 distribution (BOOTH et al. 2000; STEWART et al. 2017). The key departure from previous work is
335 that our model projects greater suitable habitat in Chiapas, Tabasco and some regions in central
336 Mexico (Figure 4 from STEWART et al. 2017) and lower suitability in the Yucatan Peninsula
337 (Figure 1 from BOOTH et al. 2000). Discrepancies may arise due to the use of different SDMs and
338 their input data. For instance, BOOTH et al. (2000) used a simple model to assess only temperature
339 and precipitation conditions in areas of South East Asia where the rust occurs then projected this
340 onto the rest of the world. For their pandemic biotype model, STEWART et al. (2017) used 137
341 records, including nursery occurrences, whereas our model was fit with 276 records, with nursery
342 data removed. A higher number of records can provide a better approximation to the potential
343 distribution of the species (PHILLIPS; DUDIK 2008) and by removing nurseries, we aimed to
344 eliminate a possible bias to microclimates affected by management and water supply that may
345 cause the projection of suitable habitat in areas with unsuitable natural rainfall conditions.
346 Further, unlike STEWART et al. (2017), we used a subset of WorldClim's 19 bioclimatic variables.

347 Despite these limitations, we considered that our model has the most updated and
348 complete occurrence data of the pandemic biotype from across the world, and provides the best
349 representation of the potential distribution of myrtle rust in Mexico based on the input data
350 (occurrence records and climate data).

351

352 **5. CONCLUSIONS**

353 The potential impact of myrtle rust is poorly understood in Mexico. Thirty-six species of
354 Myrtaceae are potentially at risk of myrtle rust infection, including species with economic and
355 ecological importance, and endangered species. Additionally, 142 species remain untested for
356 rust susceptibility and occur within the potential rust distribution. The east coast of Mexico is
357 most suitable for the rust under current and future scenarios. However, due to the ability of the
358 rust to disperse, regions of the west coast, such as Nayarit and Sinaloa are also vulnerable.
359 Veracruz, Puebla, Chiapas, Tabasco, and Oaxaca are the most vulnerable states under current and
360 all future climate scenarios. Because the occurrence records of the rust are located in Veracruz
361 and Chiapas, we encourage on-going monitoring in these regions for myrtle rust. We also suggest
362 screening to test the species with no known rust susceptibility to determine the threat to native
363 ecosystems and industries reliant on Myrtaceae. This work can be used as a basis to prioritise
364 surveillance efforts in native ecosystems and commercial plantations or conduct screening to
365 determine the susceptibility of threatened, endemic and commercial species.

366

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374

375 **COMPETING INTERESTS**

376 The authors declare that they have no conflict of interest to disclose.

377

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587

TABLES

TABLE 1. Permutation importance for the climatic variables used to model habitat suitability for myrtle rust in Mexico, using Maxent. Higher values indicate higher contribution to the model.

Climatic variable	Permutation importance
Annual Precipitation	41.1
Temperature Seasonality	33.8
Precipitation of Wettest Month	14.5
Precipitation Seasonality	7.5
Max Temperature of Warmest Month	3.1

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TABLE 2. Myrtaceae species present within the current and future suitable habitat for the pandemic biotype of myrtle rust for which rust susceptibility ratings are known. Susceptibility is based on the reaction of the host species to myrtle rust exposure reported in previous studies. The susceptibility score is given as follows (as per BERTHON et al. 2018): R = resistant, species are not infected; L = low susceptibility, infection but no sporulation; M = medium susceptibility, infection and minimal sporulation; H = high susceptibility, infection and abundant sporulation on leaves, twigs and/or fruits; S* = susceptible but severity not recorded. *Species that have a high proportion of their distribution overlapping the high-risk areas.

Species	Origin	Presence	Uses/Importance	Susceptibility	Reference for Susceptibility
<i>Acca sellowiana</i>	Introduced	Veracruz	Garden plant and fruiting tree	R	(MORIN et al. 2012)
<i>Callistemon rigidus</i>	Introduced	Morelos	Cultivation and landscaping	S*	(GIBLIN; CARNEGIE 2014)
<i>Corymbia calophylla</i>	Introduced	Michoacan	Timber, construction	R-L	(MORIN et al. 2012)
<i>Corymbia citriodora</i>	Introduced	Mexico	Essential oil used in perfumery and insect repellents	R-H	(MORIN et al. 2012)
<i>Corymbia ficifolia</i>	Introduced	Mexico	Ornamental, used in gardens, parks and streets	R-H	(MORIN et al. 2012; SANDHU; PARK 2013)
<i>Corymbia tessellaris</i>	Introduced	Mexico	For tool manufacturing	R-M	(MORIN et al. 2012)
<i>Eucalyptus amygdalina</i>	Introduced	Mexico City	Light construction, fuel for open fires, oils used for aromatherapy	R-H	(POTTS et al. 2016)
<i>Eucalyptus</i>	Introduced	Campeche, Chiapas,	Important role in	L-H	(SANDHU; PARK 2013)

<i>camaldulensis*</i>		Mexico City, Jalisco, Morelos, Mexico, Oaxaca, Puebla, Tlaxcala, Veracruz	stabilising many Australian river banks		
<i>Eucalyptus cinerea*</i>	Introduced	Mexico City, Mexico, Veracruz	Ornamental garden plant	M-H	(SANDHU; PARK 2013)
<i>Eucalyptus dunnii</i>	Introduced	Mexico	For erosion and dune control, timber, fire wood	R-M	(MORIN et al. 2012; SANDHU; PARK 2013)
<i>Eucalyptus globulus</i>	Introduced	Chiapas, Mexico City, Morelos, Mexico, Nuevo Leon, Oaxaca, Puebla, Tlaxcala, Veracruz	Used for pulpwood, timber, and herbal tea. Important source of pollen and nectar for bees	R-H	
<i>Eucalyptus gomphocephala</i>	Introduced	Mexico	Timber and furniture construction	R-H	(POTTS et al. 2016)
<i>Eucalyptus gunnii*</i>	Introduced	Chiapas	Very tolerant of cold. Ornamental	R-H	(POTTS et al. 2016)
<i>Eucalyptus populnea</i>	Introduced	Mexico	Timber, windbreak, flowers produce high quality honey	R-H	(MORIN et al. 2012)
<i>Eucalyptus punctata</i>	Introduced	Mexico	Timber, multi-coloured bark	S*	(GIBLIN; CARNEGIE 2014)
<i>Eucalyptus resinifera</i>	Introduced	Mexico City, Morelos, Mexico, Puebla	High quality timber	R-M	(MORIN et al. 2012)
<i>Eucalyptus robusta</i>	Introduced	Mexico City, Mexico, Puebla, Veracruz	Street tree. Fast growth, high flower yield, can	S*	(GIBLIN; CARNEGIE 2014)

			tolerate wide range of climate conditions		
<i>Eucalyptus saligna</i>	Introduced	Mexico	Rich honey. Coloured timber especially popular for flooring and furniture	R-M	(MORIN et al. 2012)
<i>Eucalyptus tereticornis</i>	Introduced	Chiapas, Mexico City, Morelos, Mexico, Oaxaca	Key canopy species	R-H	
<i>Eugenia uniflora</i> *	Introduced	Chiapas, Mexico City, Morelos, San Luis Potosi, Veracruz	Edible fruits and used for insect repellent	M	(MORIN et al. 2012; PEGG et al. 2014; SANDHU; PARK 2013)
<i>Lophostemon confertus</i>	Introduced	Mexico	Street tree. Smog and drought tolerant	R	(MORIN et al. 2012; SANDHU; PARK 2013)
<i>Melaleuca armillaris</i>	Introduced	Oaxaca	Cultivated as a fast-growing screening or windbreak plant	S*	(GIBLIN; CARNEGIE 2014)
<i>Melaleuca citrinus</i> * (syn. <i>Callistemon citrina</i>)	Introduced	Chiapas, Mexico City, Morelos, Mexico, Nuevo Leon, Oaxaca, Veracruz	Timber, ornamental	R-H	(MORIN et al. 2012; SANDHU; PARK 2013)
<i>Melaleuca leucadendra</i>	Introduced	Mexico, Morelos	Timber	M-H	(PEGG et al. 2014)
<i>Melaleuca quinquenervia</i>	Introduced	Jalisco	Street tree	L-H	(MORIN et al. 2012; PEGG et al. 2014; SANDHU; PARK 2013)
<i>Melaleuca salignus</i> *	Introduced	Tabasco	Landscaping	M	(PEGG et al. 2014)

(syn. *Callistemon salicina*)

<i>Myrtus communis</i>	Introduced	Sinaloa	Garden plant	M-H	(PEGG et al. 2014)
<i>Pimenta dioica</i> *	Native	Campeche, Chiapas, Hidalgo, Oaxaca, Puebla, Quintana Roo, San Luis Potosi, Tabasco, Veracruz, Yucatan	Dried unripe berries used to produce allspice	M-H	(LEÓN GALLEGOS; CUMMINS 1981; MORIN et al. 2012)
<i>Psidium cattleianum</i> *	Introduced	Nayarit, Quintana Roo, Veracruz	Commonly referred to as strawberry guava or cherry guava, produces edible fruits. Highly invasive in Hawaii	R-L	(MORIN et al. 2012)
<i>Psidium guajava</i> *	Native	Campeche, Chiapas, Guerrero, Hidalgo, Jalisco, Morelos, Mexico, Nayarit, Nuevo Leon, Oaxaca, Puebla, Queretaro, Quintana Roo, San Luis Potosi, Sinaloa, Tabasco, Tamaulipas, Veracruz, Yucatan"	Used traditionally as a medicinal plant throughout the world for a number of ailments. Commercial fruit.	R-L	(MORIN et al. 2012; SANDHU; PARK 2013)
<i>Syzygium australe</i>	Introduced	Mexico City	Common garden. Edible	R-M	(PEGG et al. 2014)

sour fruits					
<i>Syzygium cumini</i>	Introduced	Tabasco	Edible fruits. Used in alternative medicine	M	(PEGG et al. 2014)
<i>Syzygium jambos</i> *	Introduced	Chiapas, Guerrero, Hidalgo, Jalisco, Nayarit, Oaxaca, Puebla, San Luis Potosi, Tabasco, Veracruz	Fruiting tree. Wood used for charcoal. Used in traditional medicine	R-H	(LOPEZ; GARCÍA 2011; MORIN et al. 2012; PEGG et al. 2014; SANDHU; PARK 2013)
<i>Syzygium malaccense</i> *	Introduced	Chiapas, Veracruz	Fruiting tree	R	(SANDHU; PARK 2013)
<i>Syzygium megacarpum</i> *	Native	Veracruz	Fruiting tree	S*	(GIBLIN; CARNEGIE 2014)
<i>Syzygium smithii</i>	Introduced	Sinaloa	Fruiting tree. Timber is used for flooring, fittings and frames	M-H	(PEGG et al. 2014)

FIGURE

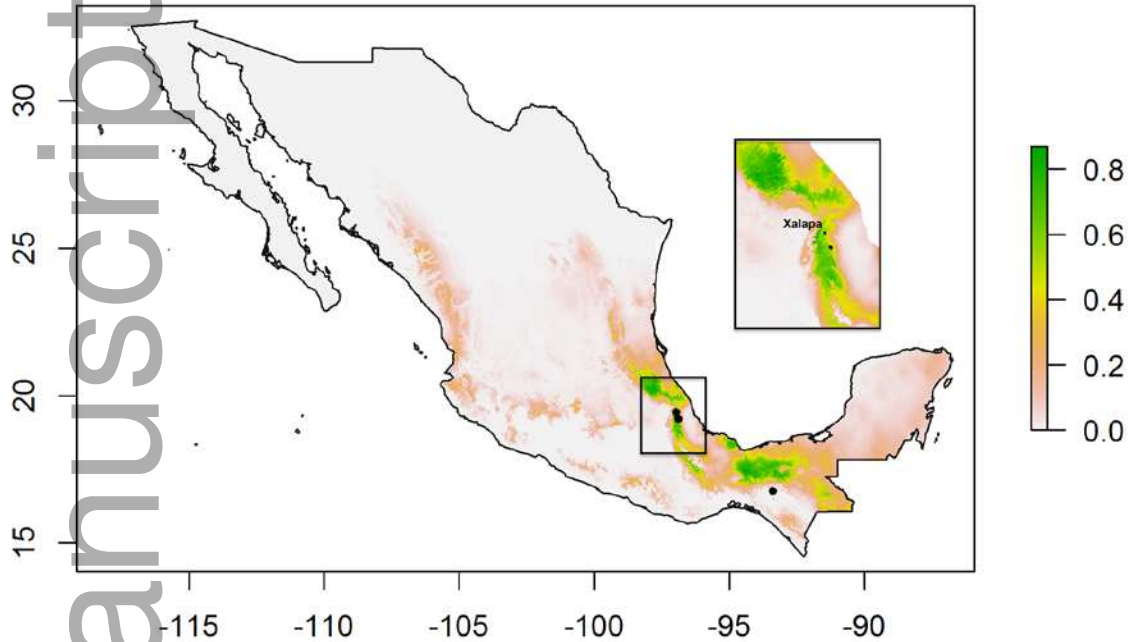


FIGURE 1. Current suitable habitat for the pandemic biotype of myrtle rust in Mexico. Areas with higher values, close to 1, are hypothesised to have greater suitability for the species. Inset: The region of highest habitat suitability with the known occurrence records (black dots) of myrtle rust.

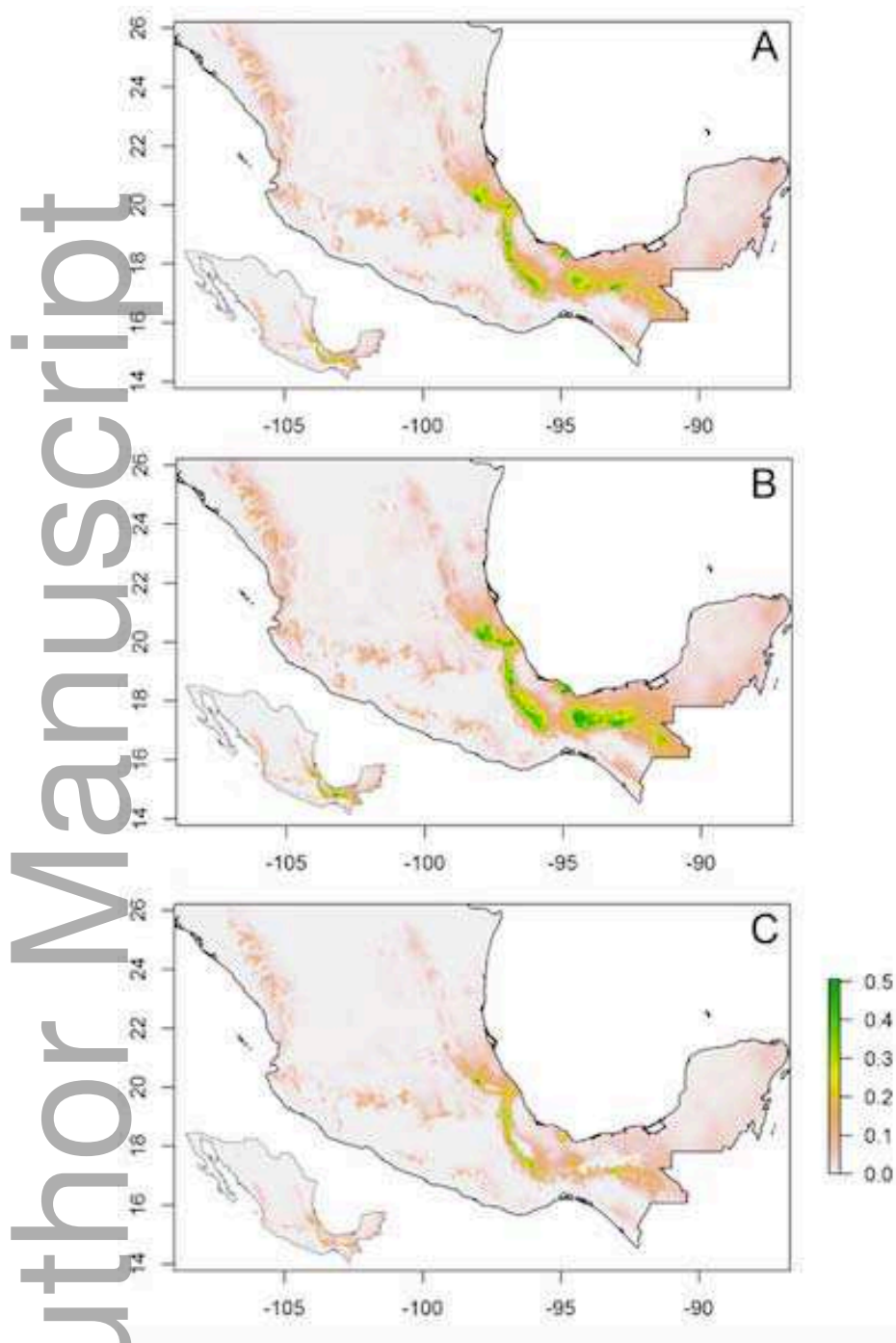


FIGURE 2. Future suitable habitat for the pandemic biotype of myrtle rust. Areas with higher values, close to 1, are hypothesised to have greater suitability for the species. Future scenarios represent the average (A) \pm standard deviation (B, and C, respectively) of projections made onto 17 climate scenarios based on RCP 8.5 (see details in Methods and full list of GCMs in Supplemental Table S2).

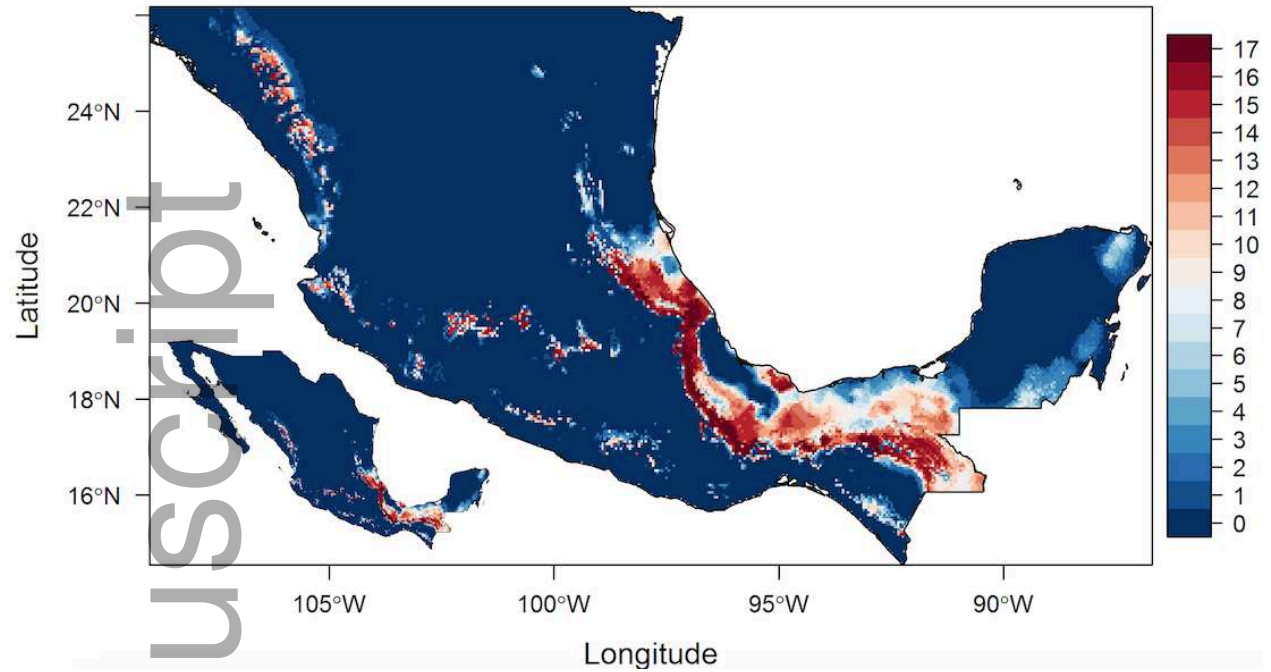


FIGURE 3. Agreement map across climate scenarios from 17 Global Circulation Models (GCM) based on RCP 8.5 (see details in Methods) for 2050. Colour scale indicates the number of scenarios in which suitable habitat for the pandemic biotype of myrtle rust is projected.