DR MANUEL ESPERON-RODRIGUEZ (Orcid ID : 0000-0003-3649-2134)

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

Manuel Esperón-Rodríguez[1,2*], John B. Baumgartner[2], Linda J. Beaumont[2], Katherine Berthon[2], Angus J. Carnegie[3], Matthew A. Alfonzetti[2], Víctor L. Barradas[4], Michelle Leishman[2]

[1] Hawkesbury Institute for the Environment, Western Sydney University, Richmond, New South Wales

[2] Department of Biological Sciences, Macquarie University, North Ryde, Australia

[3] NSW Department of Primary Industries, NSW Forest Science, Parramatta, Australia

[4] Laboratorio Interacción Planta-Atmósfera. Instituto de Ecología. Universidad Nacional Autónoma de México. 04510. México, D.F. México

*Corresponding author:
Manuel Esperón-Rodríguez
Hawkesbury Institute for the Environment
Western Sydney University, Richmond
New South Wales Ph: +61 02 4570 1925
Email: m.esperon-rodriguez@westernsydney.edu.au

Abstract

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

Key words: fungi; habitat suitability; invasive species; Maxent; fungal pathogens; species distribution model

1. INTRODUCTION

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

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

Austropuccinia psidii affects species from the Myrtaceae family (BOOTH et al. 2000). While genera and species within Myrtaceae vary in their susceptibility to this rust (BOOTH et al. 2000), it is considered a serious threat to *Eucalyptus* species (CARNEGIE; COOPER 2011; COUTINHO et al. 1998; DIANESE et al. 1984; FERREIRA 1983) and has caused extirpation of native species in ecosystems in Australia (CARNEGIE et al. 2016). In Mexico, Myrtaceae is widely distributed in temperate, tropical, and semi-arid regions (MONROY-ORTÍZ; MONROY 2006), with approximately 20 genera and 192 species—including 30 *Eucalyptus* species—distributed across the country (Global Biodiversity Information Facility, GBIF; www.gbif.org). The family is recognized for its economic and cultural importance, providing timber, fruits, spices and condiments, essential oils and nectar, and also for its medicinal and ornamental value, among others (Arellano Rodríguez et al. 2003; Cabrera et al. 2001; Monroy-Ortíz; Monroy 2006; Terán; Rasmussen 1994).

In Mexico, the negative impact of other rust fungi on natural environments and crops has been documented. Examples include the invasion of coffee rust (*Hemileia vastratix*) (López Ramírez 1998; López Ramírez; Celis 1982); *Gymnosporangium clavipes,* which infests species of the genus *Crataegus* (commonly called 'tejocote') (Alvarado-Rosales et al. 2015); and *Cronartium ribicola,* which causes white pine blister rust (López-Peralta; Sanchez-Cabrera 1996). Indeed, it is estimated that there are at least 651 rust species associated with 13 plant families in Mexico, but rusts specific to Myrtaceae is not included in this estimate (Berndt 2012; Farr; Rossman 2011; Villaseñor 2003).

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

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

2. METHODS

2.1. Occurrence records data

We undertook an exhaustive search to compile global occurrence data for *A. psidii* from a variety of sources. Specifically, we sought records from countries that have the same biotype of myrtle rust as Mexico, the pandemic biotype (MACHADO et al. 2015; STEWART et al. 2017), which include Australia, Costa Rica, Indonesia, Jamaica, Puerto Rico, and Hawaii (U.S.A.). For records in Mexico, we searched data from GBIF, the Biological Collections of the National Autonomous University of Mexico (UNIBIO), the National Commission for the Knowledge and Use of Biodiversity (CONABIO), the Global Biodiversity Information (REMIB), literature, and via personal communications (see acknowledgments). For records outside Mexico, the sources used included databases from the Australian Government (New South Wales, Queensland, Tasmania, Victoria and Northern Territory government departments), recent literature (MACHADO et al. 2015; MCTAGGART et al. 2016; POTTS et al. 2016), validated sightings from Australia's Myrtle Rust Environmental Impacts Working Group, and via personal communications. We collected a total of 2385 Australian records and 50 records of natural infection outside of Australia.

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

2.2. Modelling habitat suitability

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

We downloaded data for 19 climatic variables (**Supplemental Table S1**) from WorldClim version 1.4 (HIJMANS et al. 2005), at a resolution of 30 arc-seconds (~1 km) for model calibration. Data were projected using EPSG:4326 (longitude/latitude WGS84). We considered these data, which describe conditions for the period 1960–1990, to reflect the baseline (or current) climate. To select variables for model calibration, we evaluated correlations among climatic variables using Pearson correlation (LEGENDRE; LEGENDRE 2012) identifying pairwise combinations of variables with a correlation coefficient ≤ 0.7. We then selected three subsets of variables for model calibration based on trade-offs between biological significance and multicollinearity constraints. Of these, we selected the set that produced a climate suitability map most consistent with previous work and expert opinion. We then assessed the response curves and permutation importance generated by Maxent, and selected a final set of five variables consisting of temperature seasonality (TS), maximum temperature of the warmest month (TmaxWM), annual precipitation (AP), precipitation of the wettest month (PWM), and precipitation seasonality (PS).

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

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

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

To assess future climate suitability, we downloaded data from WorldClim for the time period 2050 (average for 2041-2060) at a resolution of 30 arc-seconds (~1 km) (EPSG:4326; longitude/latitude WGS84) (HIJMANS et al. 2005). We used scenarios from 17 global circulation models (GCMs) (**Supplemental Table S2**) and for the Representative Concentration Pathway (RCP) 8.5. RCPs are consistent with a wide range of possible changes in future anthropogenic greenhouse gas emissions. For RCP 8.5, emissions continue to rise throughout the 21st century (MEINSHAUSEN et al. 2011). We projected climate suitability for myrtle rust onto each of the 17 scenarios and calculated the average and standard deviation of these projections. We followed this approach due to the variation among different GCMs in terms of projected temperature and precipitation trends. Thus, our models represent a broad range of projected variation in future conditions. Additionally, we developed an agreement map across all 17 GCMs. This map highlights areas projected to have high habitat suitability across all possible future climates until at least 2050. For this approach, we converted the continuous suitability predictions to binary layers indicating suitable/unsuitable habitat. We used as threshold the 10th percentile for training presence/training omission (for our model, 0.0978), which assumes that 10% of the training (or test) occurrences are predicted as unsuitable (PHILLIPS et al. 2004). We acknowledge that this threshold might over-estimate habitat suitability, but because myrtle rust is an invasive species we consider this approach more valuable.

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

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

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

3. RESULTS

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

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

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

3.1. Suitable habitat for myrtle rust

We estimated current suitable habitat for the pandemic biotype of myrtle rust in Mexico to span an area of 318,442 km^2. Areas that are currently most suitable for the rust are mainly restricted to the east coast of Mexico and include regions from Nuevo Leon, Tamaulipas, Veracruz, east of San Luis Potosi, north of Puebla and Hidalgo, Oaxaca, Tabasco, Chiapas, south of Campeche, Quintana Roo, and Yucatan. From these states, the highest suitability is projected in Veracruz, Puebla, Chiapas, Tabasco, and Oaxaca. On the west coast, areas of higher vulnerability are predicted in the west of Durango, south of Sinaloa, Nayarit, Jalisco, Michoacan, Mexico, and Guerrero (**Figure 1 and Supplemental Figure S3**).

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

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

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

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

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

4. DISCUSSION

The east coast of Mexico is predicted to have the greatest expanse of suitable habitat for myrtle rust under current and future scenarios, with Veracruz and Chiapas being the most vulnerable states. This finding is consistent with the known presence of the rust in Mexico, as the only records reported for the rust are in these states. We found 36 Myrtaceae species known to be susceptible to rust infection distributed in areas that have high habitat suitability for the rust. Hence, we consider species such *Pim. dioica, S. jambos,* and *M. citrinus* to be highly vulnerable to myrtle rust. We also found 142 species with unknown susceptibility distributed within the rust's suitable habitat. Our findings highlight the potential risk to native ecosystems and commercial industries from the rust pandemic. Surveys are essential to monitor the spread of the disease in Mexico and to find the true extent of the host range.

4.1. Suitable habitat for myrtle rust

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

Future changes in precipitation and temperature will alter the distribution of suitable habitat for myrtle rust. The increase in suitability in Veracruz may be driven by the predicted increase of precipitation and cooler temperatures in some regions (Esperón-Rodríguez et al. 2016). Conversely, the projected decrease in future suitable habitat in the Yucatan Peninsula may be driven by predicted declines in precipitation (Swain; Hayhoe 2015). However, simulations show that some drier regions of Mexico (precipitation below 450 mm) may be vulnerable to rust invasion provided temperatures are not too high (Booth et al. 2000). Because temperature affects the life cycle of the rust during different spore stages (Fiqueiredo et al. 1984; Piza; Ribeiro 1989; Ruiz et al. 1987), more research is needed to understand how a future warmer climate might affect infection and germination rates and how different spore types might be favoured by warmer conditions.

It is also possible that a different biotype of myrtle rust, with a different climatic niche, may be introduced to Mexico (Stewart et al. 2017). For example, other biotypes of myrtle rust are known to severely impact eucalypt plantations in Brazil (Ferreira 1983). Similarly, *A. psidii* had been known from Jamaica for some years prior to the introduction of a new biotype that caused severe disease in allspice (*Pim. dioica*) plantations in the 1930s (MacLachlan 1938). If the rust extends its distribution, or a new biotype is introduced into Mexico via commercial ports, Myrtaceae species may be severely affected. For future climate, areas with suitable habitat for the rust in Veracruz and Nayarit might be particularly vulnerable due to their commercial activities.

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

We found 36 species of Myrtaceae —including endemic species and species of commercial importance— potentially threatened by the pandemic biotype of myrtle rust based on our model of suitable habitat for the rust and overlap with species' distributions. We consider *Pim. dioica* and *S. jambos* as the most vulnerable species to myrtle rust in Mexico. Both species are known to host *A. psidii* (León Gallegos; Cummins 1981; Lopez; García 2011; Pegg et al. 2014; Sandhu; Park 2013; Stewart et al. 2017), are reported to be severely affected by the rust (Carnegie; Cooper 2011; León Gallegos; Cummins 1981; MacLachlan 1938; Morin et al. 2012; Rao et al. 2012; Uchida; Loope 2009), a high proportion of their distributions overlaps areas with high rust suitability, and have economic value, cultural and environmental importance (Begossi et al. 2002; Liogier; Martorell 2000; Soto-Pinto et al. 2007).

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

Presently, it is difficult to account for the potential risk myrtle rust poses to members of the Myrtaceae family in Mexico, as few species in the country (19%) have been tested for susceptibility (**Tables 2 and Supplemental Table S4**). Testing species susceptibility was beyond the scope of this study, but we highlight that the presence of 142 non-tested species —including species listed as endangered or vulnerable (IUCN 2017)— throughout areas with high rust habitat suitability represent a potential risk. For these species, we recommend field surveys and screening to determine their susceptibility to myrtle rust. In regards to the *Eucalyptus* species, Mexico has an estimated of eleven million hectares of eucalypt plantations (Ruiz et al. 2006). There are 30 *Eucalyptus* species in areas containing current and future suitable habitat for the rust, but at present, only 13 have been screened for rust susceptibility (**Table 2**). Without assessing susceptibility via inoculations, the risk to these species remains unclear. Future research should be directed to test whether these species could host myrtle rust.

4.3. What are the limitations of our study?

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

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

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

5. CONCLUSIONS

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

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COMPETING INTERESTS

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

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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

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

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

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

(syn. *Callistemon salicina*)					
Myrtus communis	Introduced	Sinaloa	Garden plant	M-H	(PEGG et al. 2014)
*Pimenta dioica**	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)
*Psidium cattleianum**	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)
*Psidium guajava**	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)
Syzygium australe	Introduced	Mexico City	Common garden. Edible	R-M	(PEGG et al. 2014)

			sour fruits		
Syzygium cumini	Introduced	Tabasco	Edible fruits. Used in alternative medicine	M	(PEGG et al. 2014)
*Syzygium jambos**	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)
*Syzygium malaccense**	Introduced	Chiapas, Veracruz	Fruiting tree	R	(SANDHU; PARK 2013)
*Syzygium megacarpum**	Native	Veracruz	Fruiting tree	S*	(GIBLIN; CARNEGIE 2014)
Syzygium smithii	Introduced	Sinaloa	Fruiting tree. Timber is used for flooring, fittings and frames	M-H	(PEGG et al. 2014)

FIGURE

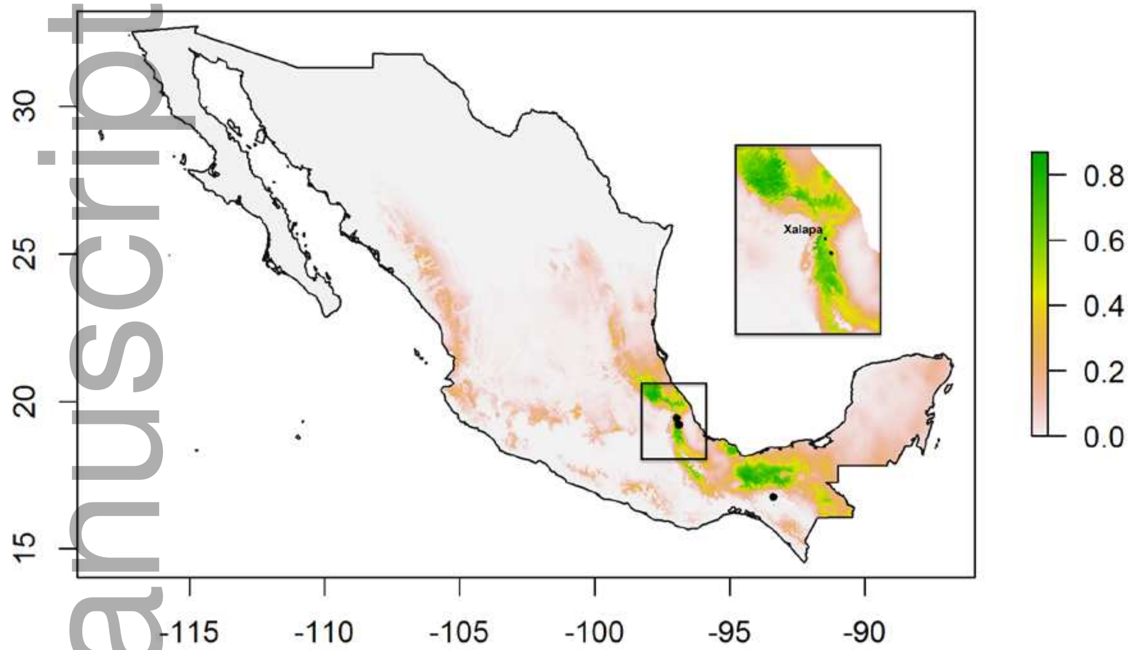

FIGURE 1. Current suitable habitat for the pandemic biotype of myrtle rust in Mexico. Areas with higher values, close to 1, are hypothesised to have greater suitability for the species. Inset: The region of highest habitat suitability with the known occurrence records (black dots) of myrtle rust.

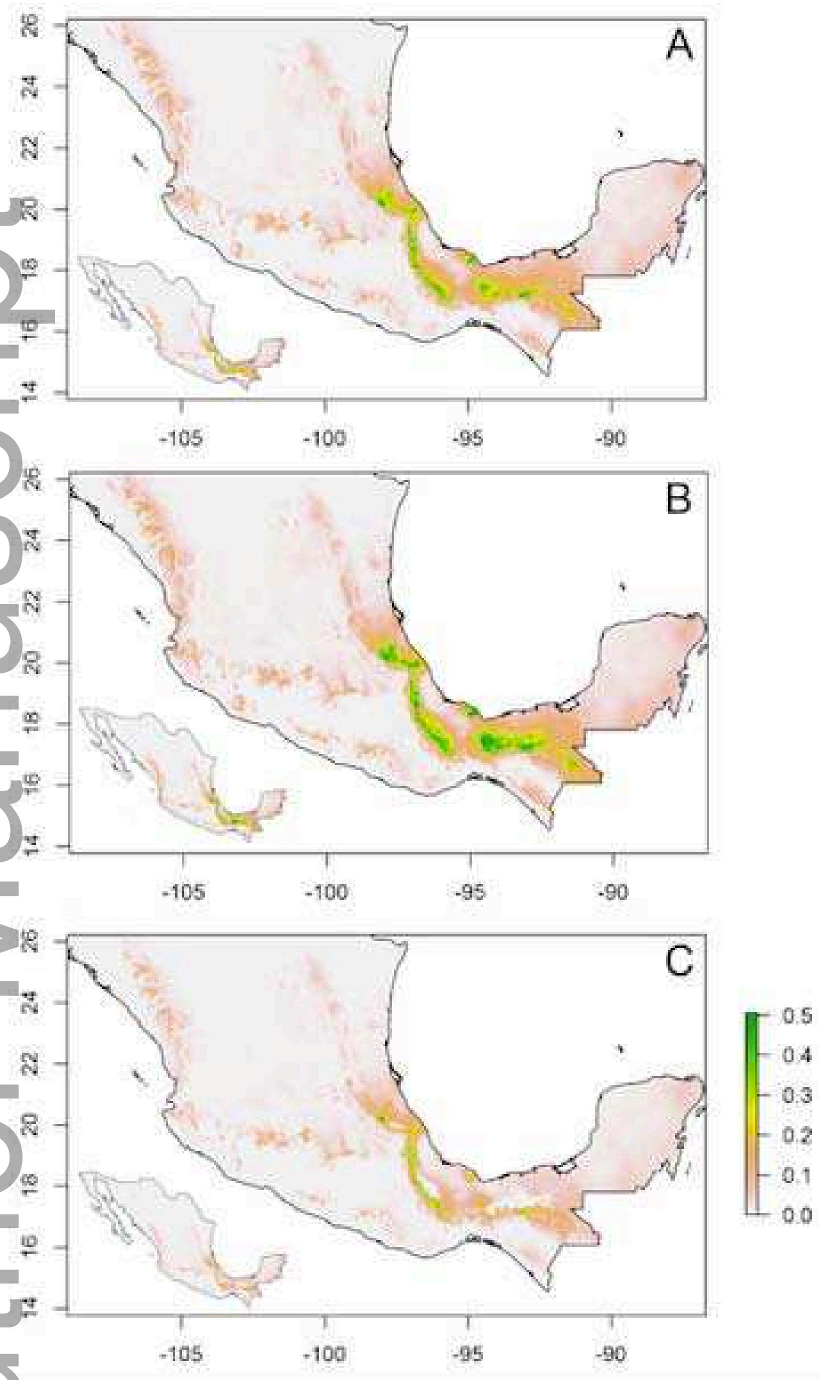

FIGURE 2. Future suitable habitat for the pandemic biotype of myrtle rust. Areas with higher values, close to 1, are hypothesised to have greater suitability for the species. Future scenarios represent the average (A) ± standard deviation (B, and C, respectively) of projections made onto 17 climate scenarios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

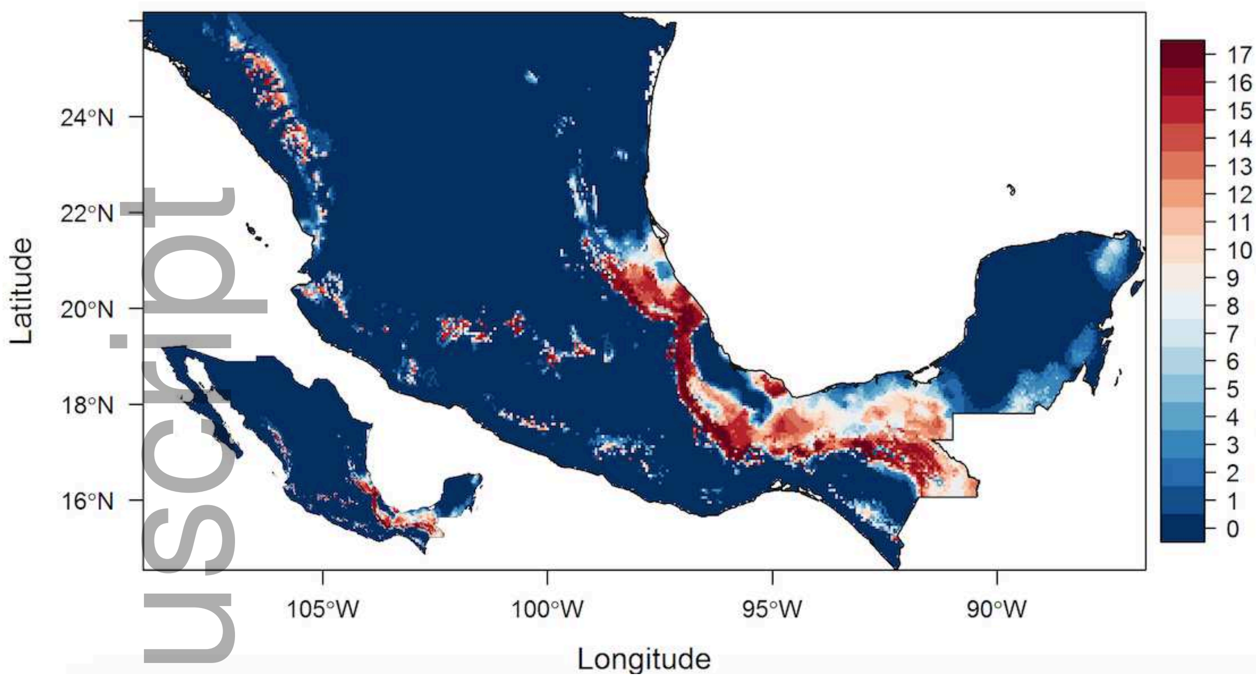

FIGURE 3. Agreement map across climate scenarios from17 Global Circulation Models (GCM) based on RCP 8.5 (see details in Methods) for 2050. Colour scale indicates the number of scenarios in which suitable habitat for the pandemic biotype of myrtle rust is projected.