

# Invasive *Syzygium jambos* trees in Puerto Rico: no refuge from guava rust

Erin Burman<sup>1,2</sup>, James D. Ackerman<sup>3,\*</sup> and Raymond L. Tremblay<sup>4,5</sup>

<sup>1</sup> El Verde Field Station, HC-05 Box 8974, Río Grande PR 00745–9601, USA

<sup>2</sup> Department of Biology, Rhodes College, Box 2338, 2000 N. Parkway, Memphis TN 38112, USA

<sup>3</sup> Department of Biology, University of Puerto Rico, P.O. Box 23360, San Juan PR 00931–3360, USA

<sup>4</sup> Department of Biology, University of Puerto Rico, P.O. Box 860, Humacao PR 00791, USA

<sup>5</sup> Center for Applied Tropical Ecology and Conservation, University of Puerto Rico, P.O. Box 23360, San Juan PR 00931–3360, USA

(Received 17 February 2017; revised 7 May 2017; accepted 10 May 2017)

**Abstract:** Biological invasions can have negative consequences for resident biota, particularly when disease-causing organisms are involved. *Austropuccinia psidii*, or guava rust, has rapidly spread through the tropics affecting both native and non-native Myrtaceae. In Puerto Rico, the rust has become common on *Syzygium jambos*, an invasive tree native to South-East Asia. What are the drivers of infection, and do refugia exist across a heterogeneous landscape? We address these questions using species distribution modelling and beta regressions. The realized and potential distribution of *Syzygium jambos* is extensive. The model produced an AUC of 0.88, with land-use categories and precipitation accounting for 61.1% of the variation. Predictability of *S. jambos* is highest in disturbed habitats, especially in mountainous regions with high precipitation. All 101 trees surveyed and measured across Puerto Rico showed signs of infection to varying extents. Infection severity was consistently associated with annual mean temperature in all top beta regression models, but was also commonly associated with tree size and precipitation variables. We found no safe sites for *S. jambos*. Many trees were extremely unhealthy and some were dead, suggesting that *S. jambos* may soon become extinct on the island or reduced to persistent stump sprouts. Native vegetation may benefit from the local demise of *S. jambos*. While the rust has not jumped to native Myrtaceae, vigilance is required, as host-shifts have occurred in other tropical regions.

**Key Words:** guava rust, invasional collapse, invasive trees, island invasions, pathogen invasion, *Puccinia*, *Syzygium*, tropical forest, tree disease

## INTRODUCTION

In native habitats, plant diseases are common, but rarely do they form epidemics with devastating consequences to host populations (Burdon 1987, Gilbert 2002, Meléndez & Ackerman 1993). However, where disease-causing organisms have invaded novel environments, epidemics can be pervasive with severe outcomes for host species and the ecosystems in which they reside (Gessler *et al.* 2011, Huang *et al.* 1998, Webber 2004). Under those circumstances, spread of diseases is dependent on a number of factors, such as host life-history stage, propagule pressure, environmental conditions and spatial heterogeneity (Gilbert *et al.* 1994, Meentemeyer *et al.* 2012, Plantegenest *et al.* 2007).

Recent outbreaks of *Austropuccinia psidii* (G. Winter) Beenken, known as myrtle, pimento or guava rust,

have had severe consequences to species of Myrtaceae throughout the tropics and subtropics, including regions where the rust has not been previously reported (Coates-Beckford & Tennant 2013, Rayamajhi *et al.* 2013, Uchida & Loope 2009). The potential for further invasions by *A. psidii* is high. Distribution modelling using climatic variables suggests that its potential distribution in the Neotropics exceeds its known range (Booth *et al.* 2000). Furthermore, the rust is genetically diverse, and different genotypes often have different sets of host species. Consequently, infection dynamics differ among regions depending on which of the genotypes are present (MacLachlan 1938, Ross-Davis *et al.* 2014).

On the Caribbean island of Puerto Rico, the *A. psidii* outbreak began in 2006 and continues to the present day, thus far only infecting *Syzygium jambos* (L.) Alston, probably reflecting a different strain than that initially reported for the island (Arthur 1915). Other than these observations, little is known of the drivers of guava

\* Corresponding author. Email: [ackerman.upr@gmail.com](mailto:ackerman.upr@gmail.com)

rust infections on Puerto Rico or elsewhere. Here we describe the geographic extent and potential spread of *A. psidii* infections on *S. jambos* in Puerto Rico. Given that the island is physiographically heterogeneous (Ewel & Whitmore 1973, López Marrero & Villanueva Colón 2006), do refugia exist for some *S. jambos* populations? Are geographic patterns of infection associated with prevailing wind direction? Is disease intensity related to environmental conditions and tree size? Epidemiological trends of infection are determined by seeking associations between intensity of rust infections and ecological conditions and tree traits. The geographic range and potential spread of *A. psidii* infections on *S. jambos* trees in Puerto Rico is expected to be extensive and follow patterns observed in literature, with trees showing signs of infection more often in warm, shaded, wet areas (Piza & Ribeiro 1988, Tessmann *et al.* 2001) and infections occurring more frequently in young trees (Coutinho *et al.* 1998). Given the prevailing winds, and the initial detection of the epidemic in eastern mountains, guava rust is expected to infect fewer trees in the western part of the island.

## MATERIALS AND METHODS

*Austropuccinia psidii* (syn. *Puccinia psidii* G. Winter; Beenken 2017) is a fungal pathogen that infects the foliage, flowers and fruit of Myrtaceae, causing defoliation and sometimes death. Originally observed on guava (*Psidium guajava* L.) in Brazil where it is thought to be native along with adjacent Uruguay, the rust is widespread in South America and has escaped the confines of its native range. It has subsequently been identified as infecting over 440 species of Myrtaceae in tropical regions across the globe (<http://www.cabi.org/isc/datasheet/45846>; Carnegie & Lidbetter 2012, Coutinho *et al.* 1998, Glen *et al.* 2007, Morin *et al.* 2012, Pegg *et al.* 2014). The rust is naturally wind-dispersed, but invasion vectors include human clothing, animals and infected plants in the plant trade (Carnegie & Cooper 2011, Carnegie *et al.* 2010, Zauza *et al.* 2014).

Since the early 20th century, guava rust has been known from Puerto Rico as an occasional disease of both *S. jambos* and *Psidium guajava* (Arthur 1915), yet only in the last decade has it become noticeable when full leaf flushes of *S. jambos* trees in Puerto Rico's El Yunque National Forest turned mustard yellow from dense blooms of urediniospores. Ross-Davis *et al.* (2014) discovered that *A. psidii* is comprised of multiple strains, each of which is genetically variable and attacks different, at times overlapping, sets of hosts. They also found that the current epidemic in Puerto Rico was caused by a particularly virulent and widespread strain of guava rust known as 'pandemic' *A. psidii*, but further genotyping is necessary

to support the conjecture that this strain is responsible for most, if not all, *S. jambos* rust infections in Puerto Rico.

*Syzygium jambos* is a myrtaceous tree native to South-East Asia that was introduced and established throughout the tropics as an ornamental and fruit tree (Janick & Paull 2008). It was present in Puerto Rico by 1811 and has since become invasive and widespread across the island (Descourtilz 1827, Little & Wadsworth 1964, Rojas-Sandoval & Acevedo-Rodríguez 2015). Although the tree can colonize mature forests, in Puerto Rico *S. jambos* is most prevalent in previously disturbed areas, particularly second-growth forests that established with the abandonment of agriculture in the mid-20th century. Where *S. jambos* has become abundant in Puerto Rico, it alters community composition and biodiversity (Brown *et al.* 2006).

We obtained *Syzygium jambos* localities from online herbarium databases of the University of Puerto Rico, Río Piedras (UPRRP), New York Botanical Garden (NY), and the University of Puerto Rico, Mayagüez (MAPR), which guided our search for *S. jambos* trees to assess and measure. Databases were accessed in June and July 2016. We surveyed 101 *S. jambos* trees across Puerto Rico, spanning a distance of ~130 km, nearly the full length of the island running from east to west. We randomly selected trees to sample, regardless of tree size or condition. During fieldwork, the data we collected on *S. jambos* included geographic coordinates of the tree, altitude, per cent shade cover (a visual estimate of the forest canopy above the tree canopy), general description of the location of the tree, basal area, canopy area (two dimensions measured and multiplied by one another), and visual estimation of the percentage of leaves showing signs of infection. All visual estimations were done by a single observer (EB).

We produced a map depicting the regions of Puerto Rico that are climatically and geographically suitable for *S. jambos* with MaxEnt species distribution modelling software, a maximum-entropy algorithm software for niche modelling (Merow *et al.* 2013, Phillips *et al.* 2006). We used climatic raster layers containing information about temperature, precipitation, altitude, humidity and other climatic data to determine predictive variables for species distribution based on species presence data from fieldwork and herbarium records of *S. jambos* occurrences. To prepare the *S. jambos* presence data for MaxEnt modelling, we removed presence points from the aggregated presence data to ensure that all points were at least 0.5 km apart to minimize pseudo-replication and sampling bias. Seventy-five points remained for MaxEnt modelling. We edited predictive variables in the form of raster maps, including the Bioclim global climatic layers dataset (<http://www.worldclim.org/current>), land-use data from the United States Department of

Agriculture Forest Service (USDA, [http://data.fs.usda.gov/geodata/other\\_fs/IITF/index.php](http://data.fs.usda.gov/geodata/other_fs/IITF/index.php)), and altitude data from the National Oceanic and Atmosphere Administration (NOAA, <http://www.ngdc.noaa.gov/dem/squareCellGrid/download/1561>) to the same extent, resolution, and format using qGIS software (<http://www.qgis.org/en/site/>). The Bioclim global climatic layers used in this study have a spatial resolution of 30 arc-seconds ( $\sim 1 \text{ km}^2$ ) (Hijmans *et al.* 2005), so we edited the altitude and land-use data to match this resolution. We clipped all environmental layers to include only Puerto Rico ( $17^\circ 48' - 18^\circ 36' \text{N}$ ,  $67^\circ 21' - 65^\circ 12' \text{W}$ ).

In creating the MaxEnt model, we ran 10 replicates with bootstrapping analysis, with 90% of the presence points randomly selected to be training points and 10% of the points selected to be test points. We chose environmental layers based on per cent contribution to the model and jackknife measure of variable importance, and the layers used in the final model included BIO\_2 (a Bioclim layer describing mean diurnal temperature range), BIO\_5 (maximum temperature of warmest month), BIO\_7 (annual temperature range), BIO\_8 (mean temperature of warmest quarter), BIO\_14 (precipitation of driest month), BIO\_15 (precipitation seasonality, coefficient of variation), BIO\_16 (precipitation of wettest quarter), BIO\_17 (precipitation of driest quarter), BIO\_18 (precipitation of warmest quarter), a land-use layer and an altitude layer. We assessed the quality of the final model via training AUC (area under the receiver operating characteristic curve), a direct measure of the relationship between the predicted distribution and the input presence points. An AUC of over 0.9 is considered to be excellent, an AUC over 0.8 is considered to be good, and AUCs below 0.7 are considered to indicate poor model performance (Franklin 2010).

To explore which factors are associated with the incidence and severity of rust infection, we first created a correlation matrix among all variables (excluding the response variable) using Kendall correlation coefficients and excluded variables that had high covariance (0.75%) to reduce collinearity. We retained the following predictive variables in the subsequent analyses: basal area, canopy area, per cent shade, annual mean temperature, annual precipitation, isothermality, mean diurnal temperature range, range of temperature seasonality and precipitation in the driest month. Subsequently, we evaluated the correlations among these variables and proportion of leaves damaged using a beta regression, which is a generalized linear model where the values are within 0 and 1. This statistical method was chosen because per cent leaf damage is non-normally distributed (and therefore unsuitable for linear regressions) and proportions have a beta distribution. Next, a complete model was constructed of all the variables using the *betareg* function from the

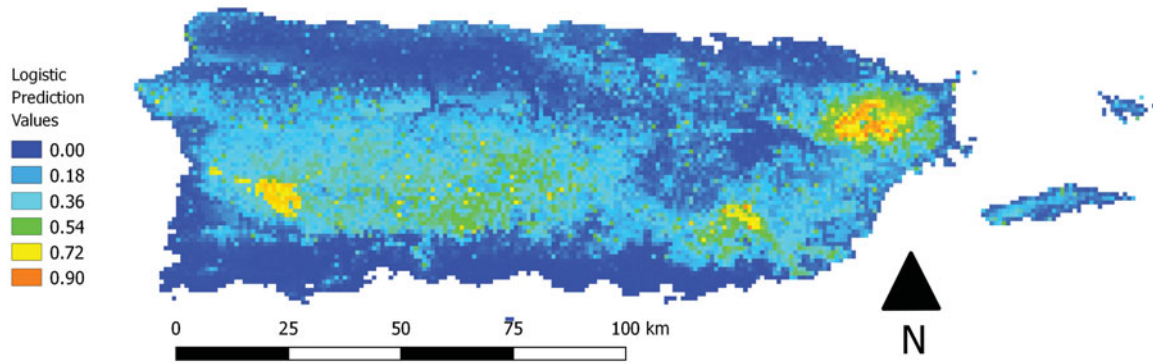
*betareg* R package (Cribari-Neto & Zeileis 2010) and subsequently all possible combination of models were evaluated using the function *dredge* in the R package *MuMIn* (<https://CRAN.R-project.org/package=MuMIn>). A total of 512 models were evaluated and the best models were chosen based on each model's corrected Akaike information criterion (AICc) value, which penalizes the more complex models. AICc values indicate the quality of a model's fit, with the lowest value corresponding to the best model. Models whose AICc values differ by less than 2 are considered very similar and these are what we report, while models with AIC differences of more than 4 are considered to be very different (Arnold 2010). There were 55 models that had a  $\Delta \text{AICc} < 4.0$ ; therefore, we proceeded to construct an average model based on weights calculated for each of these models using the *model.avg* function in the *MuMIn* package.

We also explored whether there is a geographic signature to the incidence and severity of infection across Puerto Rico. We expected an east to west pattern following the prevailing direction of the trade winds, so we performed a beta regression using just longitude as our explanatory variable and proportion of leaves damaged as our response variable.

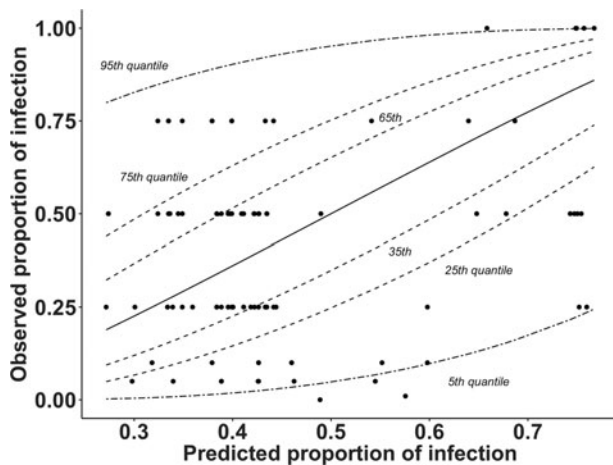
## RESULTS

The MaxEnt model had good performance with an AUC of 0.88. The environmental layers with the greatest contribution to the model were the land-use layer, with a 36.8% contribution (the land-use categories corresponding to the greatest likelihood of presence were sierra palm, transitional and tall cloud forest and artificial barrens); BIO\_16 (precipitation of wettest quarter), with a 24.3% contribution; the altitude layer, with 9.2% contribution; and BIO\_14 (precipitation of driest month) covered 8.7% of the variation. The model indicates that *S. jambos* is widespread across the island, especially in protected, mountainous areas with relatively high rainfall, such as El Yunque National Rainforest, Maricao Forest Reserve, and Carite State Forest (Figure 1). All 101 trees located in the field showed signs of guava rust infection. Thus, a MaxEnt model was not constructed for *A. psidii*, because the predicted areas of suitability would exactly match that of *S. jambos*.

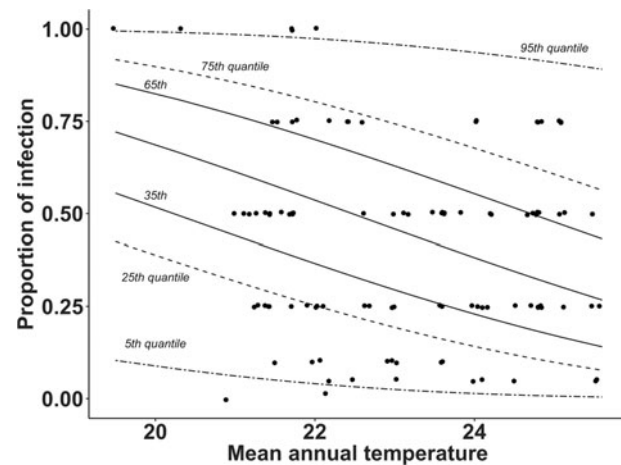
Our tree sampling produced a broad range of variation in tree and habitat variables. Average basal area was  $340 \text{ cm}^2$  (range:  $0.8 - 2463 \text{ cm}^2$ ) and average canopy area was  $33.4 \text{ m}^2$  (range:  $1.9 - 177.4 \text{ m}^2$ ). Shade above *Syzygium* canopies averaged 46% (range 0–100%), and severity of infection averaged 42% and ranged 1–100%. The best model from the beta regressions to explain the proportion of leaves damaged included annual mean temperature, mean diurnal temperature range, and mean precipitation



**Figure 1.** Species distribution model for *Syzygium jambos* and *Austropuccinia psidii* in the Caribbean island of Puerto Rico. MaxEnt model is based on *S. jambos* presence points; *A. psidii* present points overlap 100%, which would result in the same map. Warmer colours indicate areas predicted to be well suited for *S. jambos* – as well as for its parasite, guava rust, while cooler colours indicate lower suitability.



**Figure 2.** Performance of top beta regression model relative to observed data. Model explains proportion of *Syzygium jambos* leaves damaged by *Austropuccinia psidii* rust infection and includes the following variables: Annual mean temperature + Mean diurnal temperature range + Precipitation of driest month. Lines represent quantiles.



**Figure 3.** The association of annual mean temperature with the proportion of *Syzygium jambos* leaves damaged by *Austropuccinia psidii* infections. This is the driver with the greatest and most consistent influence in our top models ( $P < 0.01$ ). Lines represent quantiles.

of the driest month with all coefficients negative (Table 1). The predicted proportion of leaves damaged matched the observed, but variation was considerable (Figure 2), and only 16.5% (pseudo- $r^2$ ) of the variation was explained by this model when using a beta multiple regression. Of the three variables contained in the top model, annual mean temperature had the strongest contribution to the model, yet variation is also high (Figure 3). Our analyses also gave us 10 other models that are considered to be very similar to the top model ( $\Delta AICc < 2.0$ ). All of these models are consistent in that each one includes the variables annual mean temperature and mean precipitation of the driest month. These are the only significant variables in the average model. Trees that occur in regions that are cooler and have less precipitation in the driest month generally have greater severity of guava rust infection.

All *S. jambos* trees we inspected in our surveys showed evidence of *P. psidii* infections, so we could not compare the incidence of infection across Puerto Rico. This includes not only the trees that we measured, but also all others that we examined at each locality. However, we could compare the severity of the disease and expected that trees in the east, where the epidemic was first noticed, would be in poorer condition than those in the west. Our beta regression revealed longitude to be a poor predictor of the proportion of *S. jambos* leaves damaged (coefficient:  $-0.389$ , standard error estimate  $0.216$ ,  $z = -1.38$ ,  $P = 0.17$ ).

## DISCUSSION

Species interactions gained in novel sites can have positive effects, such as providing pollinator service to native



**Table 1.** Drivers of *Austropuccinia psidii* damage to *Syzygium jambos* leaves (proportion of leaves damaged) in Puerto Rico, 2016, based on data from 101 trees and localities. The best-performing models (ACCc < 2.0) and their ΔAICc and weights. The best-fit model is at the top of the list and the average model is at the bottom. According to the corrected Akaike information criterion (AICc), all models shown are very similar to one another. T = temperature, Ppt = precipitation. \* P < 0.05, \*\* P < 0.01.

Annual mean T	Canopy area	Annual Ppt	Iso-thermality	Mean diurnal T range	Ppt driest month	T Seasonality	Trunk area	df	AICc	ΔAICc	Weight
-0.048**				-0.064**	-0.03**			5	-21.84	0	0.06
-0.043**				-0.055*	-0.029**		0.001	7	-21.31	0.53	0.05
-0.047**	-0.01*			-0.61*	-0.03**			6	-21.26	0.58	0.05
-0.036**	-0.014**				-0.024**	0.007*	0.001*	7	-21.23	0.60	0.05
-0.037**					-0.027**		0.001	7	-20.66	1.18	0.03
-0.042**	-0.012*		-0.181*	-0.036	-0.029**	0.004	0.001	8	-20.41	1.43	0.03
-0.049**				-0.061**	-0.029**			6	-20.34	1.50	0.03
-0.045**		-0.001		-0.079**	-0.045*			6	-20.27	1.57	0.03
-0.049**				-0.052	-0.030**	0.003		6	-20.25	1.58	0.03
-0.042**			-0.199		-0.027**			5	-20.23	1.61	0.03
-0.041**	-0.004		-0.193		-0.027**			6	-19.95	1.89	0.02

species (Fumero-Cabán & Meléndez-Ackerman 2007). They may also facilitate invasions of other alien species resulting in an invasional meltdown (Ackerman *et al.* 2014, Lach *et al.* 2010, Simberloff & Von Holle 1999). *Syzygium jambos* has been a recipient of such positive interactions as its flowers are visited by both native and non-native pollinators (JDA pers. obs.), which have probably contributed significantly to its success. However, *S. jambos* has recently gained a significant negative interaction, which is an alien as well: *Austropuccinia psidii*, the guava rust. We have found that *S. jambos* occurs in small, patchily distributed populations, which are widespread across Puerto Rico. Our species distribution modelling revealed that its habitat preferences are influenced by precipitation and land-use, among other factors.

Because *A. psidii* spores are wind-dispersed, the outbreak is assumed to be fairly recent, and plants are patchily distributed, we expected variation in infection incidence and/or severity to be related to the prevailing east to west tradewinds (Brown & Hovmöller 2002). However, we found no relationship between longitude and either incidence or severity of infection. In fact, there was a non-significant trend for worse infection severities in the west. While we did not inspect every *S. jambos* tree on the island, we did search trees from near sea level to high-elevation cloud forests, and from dry to wet habitats. All trees that we encountered and inspected were infected with *A. psidii*. Either the rust dispersed very quickly, or was already ubiquitous yet latent until a stimulus triggered explosive growth drawing the attention of biologists.

Susceptibility of *Austropuccinia psidii* infections has been associated with low light, high humidity, warm temperatures and young plants (Coutinho *et al.* 1998, Piza & Ribeiro 1988, Tessmann *et al.* 2001). Consequently, we attempted to associate infection severity in *S. jambos* trees with various explanatory variables. We found that canopy cover above the *S. jambos* trees, our surrogate measure of light, was not a factor. Canopy and basal areas, our surrogates for tree age, were included among some of the top models, but neither was a significant component in the average model (Table 1). On the other hand, both temperature and precipitation variables were consistently associated with the severity of infection. All our sites fall within the temperature range ideal for urediniospore germination (Coutinho *et al.* 1998), but within this range we found that severity of infection tends to be greater at cooler temperatures (Figure 3). Presence of free water (rain) has also been associated with spore germination, and all of our sites occurred in moist and wet regions of the island. The rust appears viable wherever *S. jambos* occurs on the island; there are no safe havens for *S. jambos* in Puerto Rico.

The epidemic of guava rust in Puerto Rico is clearly severe. Many infected trees that we surveyed

were extremely unhealthy or recently dead. This is rather unusual since foliar diseases in natural tropical ecosystems generally do not cause mortality (Gilbert 2002). While all trees we observed were infected, our cross-sectional study does not permit us to distinguish among various epidemiological and pathological scenarios. For example, we do not know whether the variation in severity is due to (1) variability in resistance among trees, which can be substantial (Burdon 1987); (2) reduced virulence of the rust; (3) succession of rust strains; or (4) simply a matter of time. However, we have pieced together a hypothesis of disease progression based on our observations, those of colleagues and the literature (S. A. Cantrell 2017, D. J. Lodge 2016, A. Vale 2015, pers. comm.; MacLachlan 1938, Rayamajhi *et al.* 2013). Leaf flush in *Syzygium jambos* of Puerto Rico and elsewhere is normally a simultaneous event, and immature leaves are those that are vulnerable to the rust (Coutinho *et al.* 1998). At the onset of the rust invasion in Puerto Rico, young leaves became so infected that entire trees turned yellow-orange, soon killing the leaves. The trees responded by producing a second flush of leaves, though not as many as the first. These too became severely infected. Subsequent flushes became sporadic, confined to fewer branches, and the severity of infection in individual leaves was diminished. Meanwhile many *S. jambos* became weak as older leaves senesced and fewer younger leaves survived to maturity, perhaps creating a root-shoot imbalance. If this scenario is accurate, then *S. jambos* trees in Puerto Rico may be destined for local extinction. However, we frequently observed coppicing from the base of dead trunks, suggesting that if the trees can overcome the disease and the resulting root-shoot imbalance, then *S. jambos* may persist, perhaps relegated to the same fate as the American chestnut, which survives in most parts of its native range only as non-reproductive stump sprouts, victims of blight (Davelos & Jarosz 2004).

Given the invasiveness of *S. jambos* in the Neotropics, the implications of an extinction or near-extinction event may be beneficial to some native species, as die-off of *S. jambos* would make niche space available. However, the potential spread of the guava rust to endemic trees is of particular concern everywhere in the pathogen's invasive range, especially on islands which are generally more vulnerable to invasions than continental areas (Denslow 2003, Kueffer *et al.* 2010, Rejmánek 1996, Smith & Shurin 2006). In Puerto Rico, *S. jambos* shares its range with about 60 native species of Myrtaceae, three of which are considered endangered or critically endangered (Axelrod 2011), so the spread of guava rust to these species would constitute a conservation crisis. Similar to efforts in Australia and Hawaii (Carnegie & Cooper 2011, Loope 2010, Morin *et al.* 2012, Pegg *et al.* 2014) alien and native Myrtaceae should be monitored for *Austropuccinia psidii* infestations. We have seen that

in a short period of time, the rust can spread rapidly with devastating effects, making vigilance an important component of management strategies.

## ACKNOWLEDGEMENTS

We thank David Clark and José Sánchez for technical assistance; Wilfredo Falcón for MaxEnt training sessions; and Bianka Morales and Andrea Tirrell for field and laboratory assistance. We are also grateful for support through the Research Experience for Undergraduates programme at El Verde Field Station, University of Puerto Rico (NSF-DBI-1559679, Alonso Ramírez, Principal Investigator).

## LITERATURE CITED

- ACKERMAN, J. D., FALCÓN, W., MOLINARI, J., VEGA, C., ESPINO, I. & CUEVAS, A. A. 2014. Biotic resistance and invasional meltdown: consequences of acquired interspecific interactions for an invasive orchid, *Spathoglottis plicata* in Puerto Rico. *Biological Invasions* 16:2435–2447.
- ARNOLD, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178.
- ARTHUR, J. C. 1915. Uredinales of Porto Rico based on collections by F. L. Stevens. *Mycologia* 7:227–255.
- AXELROD, F. S. 2011. *A systematic vademecum to the vascular plants of Puerto Rico*. BRIT Press, Fort Worth. 420 pp.
- BEENKEN, L. 2017. *Austropuccinia*: a new genus name for the myrtle rust *Puccinia psidii* placed within the redefined family Sphaerophragmiaceae (Pucciniales). *Phytotaxa* 297:53–61.
- BOOTH, T. H., OLD, K. M. & JOVANOVIĆ, T. 2000. A preliminary assessment of high risk areas for *Puccinia psidii* (Eucalyptus rust) in the Neotropics and Australia. *Agriculture Ecosystems and Environment* 82:295–301.
- BROWN, J. K. M. & HOVMØLLER, M. S. 2002. Aerial dispersal of pathogens on the global and continental scales and its impact on plant disease. *Science* 297:537–541.
- BROWN, K. A., SCATENA, F. N. & GUREVITCH, J. 2006. Effects of an invasive tree on community structure and diversity in a tropical forest in Puerto Rico. *Forest Ecology and Management* 226:145–152.
- BURDON, J. J. 1987. *Diseases and plant population biology*. Cambridge University Press, Cambridge. 208 pp.
- CARNEGIE, A. J. & COOPER, K. 2011. Emergency response to the incursion of an exotic myrtaceous rust in Australia. *Australasian Plant Pathology* 40:346–359.
- CARNEGIE, A. J. & LIDBETTER, J. R. 2012. Rapidly expanding host range of *Puccinia psidii* sensu lato in Australia. *Australasian Plant Pathology* 41:346–359.
- CARNEGIE, A. J., LIDBETTER, J. R., WALKER, J., HORWOOD, M. A., TESORIERO, L., GLEN, M. & PRIEST, M. J. 2010. *Uredo rangellii*, a

- taxon in the guava rust complex, newly recorded on Myrtaceae in Australia. *Australasian Plant Pathology* 39:463.
- COATES-BECKFORD, P. L. & TENNANT, P. F. 2013. *Plant disease: the Jamaican experience*. University of West Indies Press, Kingston, Jamaica. 628 pp.
- COUTINHO, T. A., WINGFIELD, M. J., ALFENAS, A. C. & CROUS, P. W. 1998. Eucalyptus rust: a disease with the potential for serious international implications. *Plant Disease* 82:819–825.
- CRIBARI-NETO, F. & ZEILEIS, A. 2010. Beta regression in R. *Journal of Statistical Software* 34(2):1–24.
- DAVELO, A. L. & JAROSZ, A. M. 2004. Demography of American chestnut populations: effects of a pathogen and a hyperparasite. *Journal of Ecology* 92:675–685.
- DENSLow, J. S. 2003. Weeds in paradise: thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden* 90: 119–127.
- DESCOURTILZ, M. É. 1827. *Flore pittoresque et médicale des Antilles*. Volume 5. Paris. 292 pp.
- EWEL, J. J. & WHITMORE, J. L. 1973. *The ecological life zones of Puerto Rico and the U.S. Virgin Islands*. Forest Service Research Paper ITF-18. Institute of Tropical Forestry, Río Piedras. 72 pp.
- FRANKLIN, J. 2010. *Mapping species distributions: spatial inference and prediction*. Cambridge University Press, Cambridge. 340 pp.
- FUMERO-CABÁN, J. J. & MELÉNDEZ-ACKERMAN, E. J. 2007. Relative pollination effectiveness of floral visitors of *Pitcairnia angustifolia* (Bromeliaceae). *American Journal of Botany* 94:419–424.
- GESSELER, C., PERTOT, I. & PERAZZOLLI, M. 2011. *Plasmopara viticola*: a review of knowledge on downy mildew of grapevine and effective disease management. *Phytopathologia Mediterranea* 50:3–44.
- GILBERT, G. S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annual Review of Phytopathology* 40:13–43.
- GILBERT, G. S., FOSTER, R. B. & HUBBELL, S. P. 1994. Density and distance-to-adult effects of a canker disease of trees in a moist tropical forest. *Oecologia* 98:100–108.
- GLEN, M., ALFENAS, A. C., ZAUZA, E. A. V., WINGFIELD, M. J. & MOHAMMED, C. 2007. *Puccinia psidii*: a threat to the Australian environment and economy – a review. *Australasian Plant Pathology* 36:1.
- HIJMANS, R. J., CAMERON, S. E., PARRA, S. J. L., JONES, P. G. & JARVIS, A. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.
- HUANG, H., DANE, F. & KUBISIAK, T. L. 1998. Allozyme and RAPD analysis of the genetic diversity and geographic variation in wild populations of the American chestnut (Fagaceae). *American Journal of Botany* 85:1013–1021.
- JANICK, J. & PAULL, R. E. (eds) 2008. *The encyclopedia of fruit & nuts*. CABI, Wallingford. 972 pp.
- KUEFFER, C., DAEHLER, C. C., TORRES-SANTANA, C. W., LAVERGNE, C., MEYER, J.-Y., OTTO, R. & SILVA, L. 2010. A global comparison of plant invasions on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics* 12:145–161.
- LACH, L., TILLBERG, C. V. & SUAREZ, A. V. 2010. Contrasting effects of an invasive ant on a native and an invasive plant. *Biological Invasions* 12:3123–3133.
- LITTLE, E. L. & WADSWORTH, F. H. 1964. *Common trees of Puerto Rico and the Virgin Islands*. US Department of Agriculture, Washington, DC. 548 pp.
- LOOPE, L. 2010. A summary of information on the rust *Puccinia psidii* Winter (guava rust) with emphasis on means to prevent introduction of additional strains to Hawaii. US Geological Survey Open File Report 2010-1082. 31 pp.
- LÓPEZ MARRERO, T. M. & VILLANUEVA COLÓN, N. 2006. *Atlas ambiental de Puerto Rico*. Editorial de la Universidad de Puerto Rico, San Juan. 178 pp.
- MACLACHLAN, J. D. 1938. A rust of the pimento tree in Jamaica. *B.W.I. Phytopathology* 28:157–170.
- MELÉNDEZ, E. J. & ACKERMAN, J. D. 1993. The effects of rust infection on fitness components in a natural population of *Tolumnia variegata* (Orchidaceae). *Oecologia* 94:361–367.
- MEENTEMEYER, R. K., HAAS, S. E. & VÁCLAVÍK, T. 2012. Landscape epidemiology of emerging infectious diseases in natural and human-altered ecosystems. *Annual Review of Phytopathology* 50: 379–402.
- MEROW, C., SMITH, M. J. & SILANDER, J. A. 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* 36:1058–1069.
- MORIN, L., AVEYARD, R., LIDBETTER, J. R. & WILSON, P. G. 2012. Investigating the host-range of the rust fungus *Puccinia psidii* sensu lato across tribes of the family Myrtaceae present in Australia. *PLoS ONE* 7:e35434.
- PEGG, G. S., GIBLIN, F. R., MCTAGGART, A. R., GUYMER, G. P., TAYLOR, H., IRELAND, K. B., SHIVAS, R. G. & PERRY, S. 2014. *Puccinia psidii* in Queensland, Australia: disease symptoms, distribution and impact. *Plant Pathology* 63: 1005–1021.
- PHILLIPS, S. J., ANDERSON, R. P. & SCHAPIRE, R. E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190:231–259.
- PIZA, S. M. DE T. & RIBEIRO, I. J. A. 1988. Influence of light and temperature on uredospore germination of *Puccinia psidii* Winter. *Bragantia* 47:75–78.
- PLANTEGENEST, M., LE MAY, C. & FABRE, F. 2007. Landscape epidemiology of plant disease. *Journal of the Royal Society Interface* 4:963–972.
- RAYAMAJHI, M. B., PRATT, P. D., KLOPFENSTEIN, N. B., ROSS-DAVIS, A. L. & RODGERS, L. 2013. First report of *Puccinia psidii* caused rust disease epiphytic on the invasive shrub *Rhodomyrtus tomentosa* in Florida. *Plant Disease* 97:1379.
- REJMÁNEK, M. 1996. Species richness and resistance to invasion. Pp. 153–172 in Orians, G., Dirzo, R. & Cushman, J. H. (eds). *Biodiversity and ecosystem processes in tropical forests*. Springer-Verlag, New York.
- ROJAS-SANDOVAL, J. & ACEVEDO-RODRÍGUEZ, P. 2015. Naturalization and invasion of alien plants in Puerto Rico and the Virgin Islands. *Biological Invasions* 17:149–163.
- ROSS-DAVIS, A. L., GRAÇA, R. N., ALFENAS, A. C., PEEVER, T. L., HANNA, J. W., UCHIDA, J. Y., HAUFF, R. D., KADOOKA, C. Y., KIM, M. E., CANNON, P. G., NAMBA, S., MINATO, N., SIMETO, S., PÉREZ, C. A., RAYAMAJHI, M. B., MORÁN, M., LODGE, D. J., ARGUEDAS, M., MEDEL-ORTIZ, R., LÓPEZ-RAMÍREZ, M. A., TENNANT, P., GLEN, M.

- & KLOPFENSTEIN, N. B. 2014. Tracking the distribution of *Puccinia psidii* genotypes that cause rust disease on diverse myrtaceous trees and shrubs. Pp. 131–137 in Chadwick, K. (ed.). *Proceedings of the 61st Annual Western International Forest Disease Work Conference, Waterton Lakes National Park, Alberta*. U.S. Department of Agriculture, Forest Service, Forest Health Protection, Washington, DC.
- SIMBERLOFF, D. & VON HOLLE, B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1:21–32.
- SMITH, S. A. & SHURIN, J. B. 2006. Room for one more? Evidence for invasibility and saturation in ecological communities. Pp. 423–447 in Cadotte, M. W., McMahon, S. M. & Fukami, T. (eds). *Conceptual ecology and invasion biology*. Springer, Dordrecht.
- TESSMANN, D. J., DIANESE, J. C., MIRANDA, A. C. & CASTRO, L. H. R. 2001. Epidemiology of a Neotropical rust (*Puccinia psidii*): periodical analysis of the temporal progress in a perennial host (*Syzygium jambos*). *Plant Pathology* 50:725–731.
- UCHIDA, J. Y. & LOOPE, L. L. 2009. A recurrent epiphytotic of guava rust on rose apple, *Syzygium jambos*, in Hawaii. *Plant Disease* 93:429.
- WEBBER, J. F. 2004. Experimental studies on factors influencing the transmission of Dutch elm disease. *Investigacion Agraria Sistemas y Recursos Forestales* 13:197–205.
- ZAUZA, E. A. V., LANA, V. M., MAFFIA, L. A., ARAUJO, M. M. F. C., ALFENAS, R. F., SILVA, F. F. & ALFENAS, A. C. 2014. Wind dispersal of *Puccinia psidii* urediniospores and progress of eucalypt rust. *Forest Pathology* 45:102–110.