

Assessing the Potential for Establishment of Western Cherry Fruit Fly Using Ecological Niche Modeling

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ABSTRACT Sweet cherries, *Prunus avium* (L.) L., grown in the western United States are exported to many countries around the world. Some of these countries have enforced strict quarantine rules and trade restrictions owing to concerns about the potential establishment and subsequent spread of western cherry fruit fly, *Rhagoletis indifferens* Curran (Diptera: Tephritidae), a major quarantine pest of sweet cherry. We used 1) niche models (CLIMEX and MaxEnt) to map the climatic suitability, 2) North Carolina State University–Animal and Plant Health Inspection Service Plant Pest Forecasting System to examine chilling requirement, and 3) host distribution and availability to assess the potential for establishment of *R. indifferens* in areas of western North America where it currently does not exist and eight current or potential fresh sweet cherry markets: Colombia, India, Indonesia, Malaysia, Taiwan, Thailand, Venezuela, and Vietnam. Results from niche models conformed well to the current distribution of *R. indifferens* in western North America. MaxEnt and CLIMEX models had high performance and predicted climatic suitability in some of the countries (e.g., Andean range in Colombia and Venezuela, northern and northeastern India, central Taiwan, and parts of Vietnam). However, our results showed no potential for establishment of *R. indifferens* in Colombia, Indonesia, Malaysia, Taiwan, Thailand, Venezuela, and Vietnam when the optimal chilling requirement to break diapause (minimum temperature $\leq 3^{\circ}\text{C}$ for at least 15 wk) was used as the criterion for whether establishment can occur. Furthermore, these countries have no host plant species available for *R. indifferens*. Our results can be used to make scientifically informed international trade decisions and negotiations by policy makers.

KEY WORDS CLIMEX, insect pest, MaxEnt, NAPPFAST, niche modeling

The introduction and spread of exotic plant pests and diseases is heavily influencing our food safety, trade, market access, market development, and net profit and sustainability (Pimentel 2002). Increased global trade, tourism, and transportation have accelerated the spread of insect pests and other invasive species. Many countries around the world have imposed quarantine restrictions to safeguard against the inadvertent introduction and spread of invasive species (U.S. Department of Agriculture–Foreign Agricultural Service [USDA–FAS] 2014). For example, in the United States, the U.S. Department of Agriculture–Animal Plant and Health Inspection Service (USDA–APHIS) inspected cargo and baggage arriving at U.S. ports-of-entry and border crossings during 1972–2003. McCullough et al. (2006) summarized >700,000 pest interceptions recorded in the Port Information Network database from 1984 to 2000 and found that insects dominated the database with 73–84% of the annual records; the majority of these belong to the orders Homoptera, Lepidoptera, and Diptera. Not all non-

native species arriving in a new region become invasive pests (Williamson 1996); the majority do not survive, reproduce, and establish viable populations owing to adverse climatic conditions, host unavailability, and phenological mismatches between insect and host plant species.

The western cherry fruit fly, *Rhagoletis indifferens* Curran (Diptera: Tephritidae), is a major quarantine pest of sweet cherry, *Prunus avium* (L.) L., in the western United States that could potentially be an invasive species within areas of the United States where it does not currently exist or in other countries. *R. indifferens* is found from southern British Columbia in the north through southern California in the United States (Mackie 1940, Frick et al. 1954, Blanc and Kiefer 1955, Bush 1966, Senger et al. 2009, Dowell and Penrose 2012). The fly's major native host is bitter cherry [*Prunus emarginata* (Douglas) Eaton; Curran 1932], which is distributed predominantly in the ponderosa pine and coastal forest ecosystems in the western United States and southwestern Canada (Bush 1966, Lyons and Merilees 1995). Bitter cherry does not occur on other continents. *R. indifferens* has been found to infest 15 plant species in western North America (Yee 2008, Yee and Goughnour 2008, Yee et al. 2013).

R. indifferens has never been reported in the tropical countries of Colombia, Indonesia, Malaysia, Tai-

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wan, Thailand, Venezuela, and Vietnam. This could be because those regions are too hot to meet chilling requirement for *R. indifferens* to complete development and break diapause. Most individuals of *R. indifferens* require at least 15 wk of chilling (minimum temperature $\leq 3^{\circ}\text{C}$) to break diapause (Frick et al. 1954; van Kirk and AliNiazee 1981, 1982). Postdiapause developmental rate of pupae increases until 28°C , after which development diminishes (Stark and AliNiazee 1982). *R. indifferens* pupae overwinter in the soil under the host species and emerge in May through August. Therefore, soil temperature and moisture play a critical role in pupal development and adult emergence (Yee 2013). Despite this, cherry growers in the western United States that currently ship (or are interested in shipping) cherries to Colombia, India, Indonesia, Malaysia, Taiwan, Thailand, Venezuela, and Vietnam must maintain an active control program for *R. indifferens* that includes monitoring through trapping and adherence to strict pesticide application schedules and stringent quarantine protocols. Successful establishment of an insect pest in an area is generally affected by both biotic and abiotic factors. Biotic factors include the availability of host or food sources and the presence of competing species. Host availability is a prerequisite for insect pest survival, reproduction, and establishment in a novel environment (Niemella and Matteson 1996). Abiotic factors include climate of the area (e.g., temperature and humidity; Watts and Worner 2006, Leung et al. 2012) and whether species-specific temperature thresholds (e.g., chilling requirements for some species to break or start diapause) are met. Soil type and soil moisture can also be important for insects that complete part of their life stages underneath the soil. Temporal and seasonal matching of insect emergence and flowering or fruiting of host plant species also play a crucial role in insect pest establishment. In addition to host availability, climatic suitability, and other biotic and abiotic factors, propagule pressure (i.e., the number of individuals of an insect pest introduced to a new region), and photoperiod (i.e., daylength experienced by a species) may also play a critical role in pest establishment (Saikkonen et al. 2012, Bacon et al. 2014).

Ecological niche models (ENMs) and species distribution models are increasingly being used in several areas of ecology, including biogeography, climate change, species invasions, conservation planning, and pest risk analyses (Franklin 2009, Venette et al. 2010, Peterson et al. 2011, Elith and Franklin 2013). ENMs can be classified into two broad categories: 1) correlative models and 2) process-based mechanistic models (Dormann et al. 2012). Correlative niche models (e.g., MaxEnt) integrate species occurrence data with spatial environmental data layers and produce maps of probability of presence or relative habitat suitability for a species. The process-based mechanistic niche models (e.g., CLIMEX) use species functional traits and physiological tolerances for model fitting. Correlative models generally perform poorly when making projections under novel conditions (Webber et al. 2011). However, the projections can be improved by

fitting these models using biologically informed, hypothesis-driven variables. These models are also relatively easy to implement, simple and flexible in data requirements, and can be fitted using existing species occurrence data from museums and herbaria (Kearney et al. 2010, Elith and Franklin 2013). Both types of niche models have been used to study the risk of insect pest establishment (e.g., De Meyer et al. 2010, Wang et al. 2010, Evangelista et al. 2011, Lozier and Mills 2011, Ni et al. 2012, Parsa et al. 2012, de Villiers et al. 2013). However, a majority of these studies considered only climatic suitability and did not include host availability. The pest risk maps produced by niche models can be used by policy makers for developing international trade decisions and negotiations, imposing domestic quarantines, conducting biosecurity surveillance, or responding to pest incursions (Kriticos et al. 2013).

The objectives of this study were to 1) develop potential distribution maps for *R. indifferens* in its native range (i.e., western North America) using the correlative model MaxEnt and the process-based mechanistic niche model CLIMEX; 2) project these models to eight countries that are current or potential fresh sweet cherry markets to assess the potential for establishment of *R. indifferens*; these are Colombia, Venezuela, India, Indonesia, Malaysia, Taiwan, Thailand, and Vietnam; 3) identify abiotic factors that affect *R. indifferens* distribution in its native range; and 4) map host plant availability for *R. indifferens* in its native range and the eight tropical countries.

Materials and Methods

***R. indifferens* Occurrence Data.** To capture the entire range of environmental conditions, *R. indifferens* occurrence data were collected from western North America (its current distributional range). We gathered *R. indifferens* presence records from published articles and reports and books, including Banham (1971, 1973), Zwick et al. (1977), AliNiazee (1978), Kroening et al. (1989), Messina (1990), Jones et al. (1991), Yee (2005, 2006, 2008), Yee and Alston (2006), Yee and Goughnour (2008), Maxwell et al. (2009), Senger et al. (2009), Yee et al. (2010, 2011), and Dowell and Penrose (2012). Five presence records were obtained from the Global Biodiversity Information Facility (GBIF) Web site (<http://data.gbif.org>). Three presence records for Utah were collected from Utah State University's Cooperative Extension Web site (<http://utahpests.usu.edu/ipm/files/uploads/PPTDocs/04sh-insects-wcfffcontrol.pdf>). Where exact latitude and longitude data were not provided, Google Maps (<http://maps.google.com/>) were used to record geographic coordinates of locations (using the "What's here?" feature). *R. indifferens* occurrence data published in Foote et al. (1993) (Map 68; page 339) were digitized using ArcGIS (ESRI Inc. 2012). In total, 205 records were collected covering the entire range of *R. indifferens* distribution that included eight western U.S. states and southern British Columbia, Canada (Fig. 1a, Supp Fig. 1 [online only]). Duplicate occurrence records were removed, and the

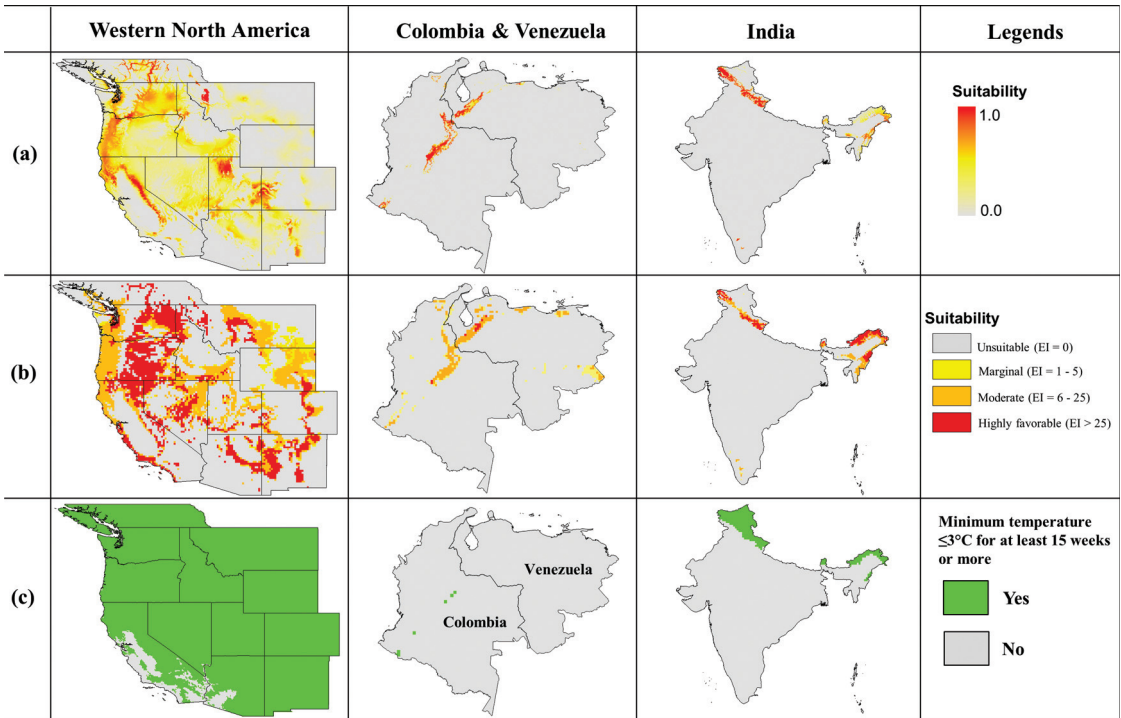


Fig. 1. Projected potential distribution or climatic suitability for *R. indifferens* in western North America, Colombia, Venezuela, and India using (a) MaxEnt, (b) CLIMEX; and (c) chilling requirement map for *R. indifferens* (minimum temperature $\leq 3^{\circ}\text{C}$ for ≥ 15 wk) using NAPPFAST.

remaining 184 spatially unique (one record per 5- by 5-km cell) records were used in spatial modeling and other analyses.

Host Plant Species Distribution Data. Fifteen plant species have been recorded as hosts of *R. indifferens* (Yee 2008, Yee and Goughnour 2008). These plant species can be divided into three broad categories based on their level of use by *R. indifferens* in the field: 1) Major hosts (used most commonly; 50–100% samples infested; Yee 2008, Yee and Goughnour 2008)—bitter cherry (*P. emarginata*), sweet cherry (*P. avium*), sour cherry (*Prunus cerasus* L.), mahaleb cherry (*Prunus mahaleb* L.), bird cherry (*Prunus padus* L.); 2) Minor or Rare hosts (<50% but >1% samples infested)—choke cherry (*Prunus virginiana* L.), pin cherry (*Prunus pennsylvanica* Ehrhart), cherry Laurel (*Prunus laurocerasus* L.), cherry Plum (*Prunus cerasifera* Ehrhart), cascara (*Rhamnus purshiana* de Cundolle); and 3) Incidental hosts (<1% fruits infested)—apricot (*Prunus armeniaca* L.), black hawthorn (*Crataegus douglasii* Lindley), Japanese plum (*Prunus salicina* Lindley), Pacific plum (*Prunus subcordata* Benth), and Chinese crabapple (*Malus spectabilis* (Aiton) Borkhausen). Distribution data for the native host, bitter cherry, were acquired from GBIF, Intermountain Region Herbarium Network (<http://intermountainbiota.org/portal/index.php>), Calflora (<http://www.calflora.org/>) and E-Flora of British Columbia (<http://www.geog.ubc.ca/biodiversity/eflora/>). Global distribution data for the other 14 host plants were obtained from the

GBIF Web site. Because of the large number of occurrence records for some host species, data were mapped at 1-degree resolution.

Environmental Data. Twenty-nine environmental variables were considered as potential predictors of *R. indifferens* distribution (Supp Table 1 [online only]). These variables were chosen based on the fly's biology and ecological requirements, and similar niche modeling studies on other fruit flies and insects (e.g., Li et al. 2009, De Meyer et al. 2010, Sambaraju et al. 2012). These variables included climatic, topographic, and species-specific phenology variables. Nineteen Bioclim variables were obtained from the WorldClim dataset (<http://www.worldclim.org>; Hijmans et al. 2005). Three phenology variables for *R. indifferens* were calculated based on its lower development threshold and chilling requirements: number of degree-days with average temperatures at or above 8.3°C (van Kirk and AliNiazee 1981), number of degree-days with average temperatures at or below 3°C and 5°C (chilling requirement; Frick et al. 1954; van Kirk and AliNiazee 1981, 1982), using monthly temperature data layers in "Raster Calculator" in ArcGIS version 10.1 (ESRI Inc. 2012). Direct solar radiation, elevation, and potential evapotranspiration were also included (Supp Table 1 [online only]). Bioclimatic variables were obtained at ≈ 5 -km spatial resolution to account for potential spatial inaccuracies during digitization of presence records from the published maps (e.g., Foote et al. 1993). Other layers obtained at 1-km resolution

were resampled to ≈ 5 -km resolution to match with the 19 bioclimatic variables.

The North Carolina State University–APHIS Plant Pest Forecast (NAPFFAST) system was used to investigate whether different countries met the optimal chilling requirement that results in the major synchronized emergence of *R. indifferens*. The NAPFFAST system is an Internet-based online tool for plant pest modeling using the latest global geo-referenced climatological weather data (<http://www.nappfast.org/>; Magarey et al. 2007). Chilling requirement maps for different countries were generated using minimum daily temperature ($\leq 3^{\circ}\text{C}$ for ≥ 105 days) records from the past 10 yr (1 July 2003–30 June 2013) using the NAPFFAST system. The NAPFFAST system has higher temporal resolution (daily and weekly) and more up-to-date climatic data than WorldClim (monthly averages; 1950–2000) and CLIMEX (weekly; 1961–1990).

Climate Suitability Modeling. Two commonly used niche models—MaxEnt and CLIMEX—were used to model climatic habitat suitability for *R. indifferens* in its native range and eight countries that are current or potential fresh sweet cherry markets.

Correlative Niche Modeling Using MaxEnt. MaxEnt (version 3.3.3k; Phillips et al. 2006, Elith et al. 2011) was used because of its better predictive performance than other ENMs, and its use in previous potential distribution modeling studies on insect pests and other species of concern (Elith et al. 2006, Li et al. 2009, Kumar et al. 2009, De Meyer et al. 2010). MaxEnt is a general purpose, machine learning, nonparametric, predictive model that uses the presence-only data (locations where species are present); it does not require species absence data (Phillips et al. 2006). This method estimates the probability distribution of a species by finding the probability distribution of maximum entropy, which is a probability that is closest to uniform (Phillips et al. 2006). Initial model was run with default settings in MaxEnt, which resulted in highly complex models and nonsensical species response curves. Then MaxEnt was run with different values of regularization parameter ($L = 1.5$ and 2.0) and leaving other settings at default but that also resulted in quite a complex model. As a result, the MaxEnt's default settings were changed and only linear, quadratic, and product features were used to keep the models simple and avoid overfitting. The “fade-by-clamping” option was used to avoid model projections outside the environmental range of the training data. The “jackknife” feature in MaxEnt was used to evaluate the relative influence of different environmental predictors on *R. indifferens* distribution. The MaxEnt-generated species “Response Curves” that show the relationships between predicted probabilities of presence for a species and different environmental predictors were also examined.

All environmental variables were examined for cross-correlations to address the multicollinearity issue. Only one variable from each set of highly correlated predictors (Pearson correlation coefficient, $r > 0.75$ or < -0.75) was included in the model. The decision to include or exclude a highly correlated variable was made based on

its biological relevance to *R. indifferens*, ease of interpretation, and its relative predictive power (based on training gain in the preliminary MaxEnt model). For example, degree-day with average temperature $\geq 8.3^{\circ}\text{C}$ and annual potential evapotranspiration were highly correlated ($r > 0.85$; $P < 0.0001$), so the latter was dropped and the former included.

Sampling Bias, Background Selection, And Spatial Autocorrelation. Because *R. indifferens* occurrence data were not collected randomly, potential sampling bias was corrected by drawing 10,000 random background points (or pseudoabsences) using a kernel density estimator (KDE) surface (see Supp Fig. 1 [online only]). The KDE surface was generated using all the occurrence data points in Arc GIS with the “kernel density” and the “create spatially balanced points” tools in Arc Tools. Thus, the background data points had the same sampling bias as species occurrences. The model was trained for the native range of *R. indifferens* (i.e., western North America) and projected to the eight tropical countries.

Moran's *I* correlograms were generated to examine spatial autocorrelation in model residuals (1—predicted probability of presence; De Marco et al. 2008) using the “sp.correlogram” function in the “spdep” package in R (R Development Core Team 2012). Significance of Moran's *I* was tested using a two-sided *P* value; values were adjusted for multiple testing using Bonferroni corrections. No significant spatial autocorrelation was detected in *R. indifferens* model residuals at any of the lag distances (Supp Fig. 2 [online only]).

Model Selection, Evaluation, and Validation. Eighty percent of occurrence data were used for training ($n = 147$) the MaxEnt models and remaining 20% for independent validation of model performance. Akaike's Information Criteria (AIC) and the information-theoretic approach (Burnham and Anderson 2002) were used to evaluate multiple models and select the “best” models for *R. indifferens*. ENMTools (Warren et al. 2010) were used to calculate AIC_c (AIC corrected for small sample sizes) for different MaxEnt models. The models were ranked by calculating differences in AIC_c values as $\Delta\text{AIC}_{ci} = (\text{AIC}_{ci} - \text{minimum AIC}_c)$. The best model has $\Delta\text{AIC}_{ci} = 0$ and only the models with $\Delta\text{AIC}_{ci} \leq 2$ have substantial support (Burnham and Anderson 2002). We evaluated four MaxEnt models: MaxEnt_Env (model with only environmental variables); MaxEnt_EnvDef (MaxEnt_Env with default settings), MaxEnt_EnvClimex (MaxEnt_Env and CLIMEX), and MaxEnt_Climex (model with only CLIMEX outputs as predictors).

The commonly used metric AUC or area under the receiver operating characteristic (ROC) curve (Fielding and Bell 1997, Phillips et al. 2006) was used as one of the measures for evaluating model performance. The AUC is a threshold-independent measure of a model's ability to discriminate presence from absence (or background). AUC value of 0.5 shows that model predictions are not better than random; values < 0.5 are worse than random; 0.5–0.7 indicate poor performance; 0.7–0.9, reasonable or moderate performance; and > 0.9 , high performance (Peterson et al. 2011).

Table 1. Parameters used for *R. indifferens* distribution modeling using CLIMEX values were chosen based on Jones et al. (1991), Song et al. (2003), van Kirk and AliNiazee (1982), Frick et al. (1954), Stark and AliNiazee (1982), and Yee (2013)

Parameter	Description	Value
Temperature Index (TI)		
DV0	Lower temp threshold for growth	3°C
DV1	Lower optimum temp for growth	5°C
DV2	Upper optimum temp for growth	25°C
DV3	Upper temp threshold for growth	28°C
PDD	Number of degree-days above DV0 needed to complete one generation	1800
Moisture Index (MI)		
SM0	Lower soil moisture threshold	0.0 ^a
SM1	Lower optimum soil moisture	0.10 ^a
SM2	Upper optimum soil moisture	0.60 ^a
SM3	Upper soil moisture threshold	0.76 ^a
Cold Stress (CS)		
TTCs	Temperature threshold for cold stress	-6.0°C
THCS	Cold stress accumulation rate	-0.001 wk ⁻¹
Heat Stress (HS)		
TTHS	Temperature threshold for heat stress	28°C
THHS	Heat stress accumulation rate	0.01 wk ⁻¹
Dry Stress (DS)		
SMDS	Soil moisture threshold for dry stress	0.0 ^a
HDS	Dry stress accumulation rate	0.0 wk ⁻¹
Wet Stress (WS)		
SMWS	Soil moisture threshold for wet stress	0.76 ^a
HWS	Wet stress accumulation rate	0.001 wk ⁻¹

^a Threshold expressed as a proportion of soil moisture holding capacity (0 = oven dry, and 1 = field capacity [saturation]). Values >1.0 indicate the possibility of excessive amounts of rainfall and soil moisture.

The 10-fold cross-validation procedure in MaxEnt was used on 80% training data; averaged test AUC values across the 10 replicates (AUC_{cv}) were reported. In addition, Pearson correlation coefficient between “presences-random background” and predicted probabilities of presence was also used to evaluate MaxEnt models (Elith et al. 2006).

Model validation was performed using 20% withheld presence data ($n = 37$) for *R. indifferens* in western North America. The AUC_{cv}, the partial AUC ratio statistic, and sensitivity (fraction of correctly predicted presences) values were calculated using the above independent dataset. The partial AUC ratio statistic (Peterson et al. 2008) was calculated using a Visual Basic program (Barve, <http://biodiversity-informatics-training.org>). Test sensitivity was calculated at 0% training omission rate (or lowest predicted threshold [LPT]), 2% training omission rate, and 5% training omission rate. Zero percent omission rate means 100% of the training presence locations fall inside the suitable habitat, and 5% training omission rate means 5% of the training localities fall outside the suitable habitat (see more details in Liu et al. (2013)).

Process-Based Niche Modeling Using CLIMEX. CLIMEX 3.0 (Sutherst et al. 2007) was used to develop a mechanistic simulation model to estimate the climatic suitability for the establishment of *R. indifferens* in western North America. It calculates a weekly growth index that describes the potential for population growth and development using optimal and limiting conditions of temperature and moisture; more details are provided in Sutherst et al. (2007) and Ireland et al. (2013).

The “Compare Locations” function in CLIMEX was used to develop the simulation model for *R. indifferens*

that calculated an annual index of climatic suitability for a species by combining growth index, stress indices, and stress interaction indices (Sutherst et al. 2007). The recently published CliMond CM10_1975H_V1 climatic dataset (Kriticos et al. 2012; available at <http://www.climond.org>) interpolated at 10 arc minute (≈ 18 km) resolution was used for CLIMEX modeling. This dataset has long-term monthly climate means centered on 1975 for precipitation, maximum temperature, minimum temperature, and relative humidity at 0900 and 1500 hours. CLIMEX generates an index of climatic suitability for the species called the Ecoclimatic Index (EI) that varies from 0 to 100, where 0 represents locations that are unfavorable for long-term survival of the species and values close to 100 indicate areas that have optimal conditions for the species’ growth year round. Following Kriticos et al. (2003), EI values were classified into four arbitrary categories: unsuitable (EI = 0), marginal (EI = 1–5), moderately favorable (EI = 6–25), and highly favorable (EI > 25). The localities with EI > 0 were interpreted as correctly predicted presences. Sensitivity metric was calculated using 20% withheld data.

Fitting CLIMEX Parameters. Values for CLIMEX model parameters were defined based on published laboratory studies and phenological observations on physiological tolerances of *R. indifferens* and were iteratively adjusted until the simulated distribution matched the known distribution of *R. indifferens* in western North America (Table 1).

Degree-Days Per Generation (PDD). The degree-day (DD) accumulation requirement for the completion of one generation of *R. indifferens* was set to 1800 based on a 5°C lower optimum temperature threshold for growth (Jones et al. 1991, Song et al. 2003). Jones et al. (1991) detected first average fly emergence (based on

Table 2. Summary of *R. indifferens* model selection and evaluation

Model (<i>n</i> = 184)	Model description Variables	No. of variables	No. of parameters in MaxEnt model	Model selection			Model evaluation	
				AIC _c	Δ AIC _c	Model rank	Avg. test AUC _{cv}	Pearson correlation coefficient (<i>r</i>)
MaxEnt_Env	Degree-day8.3, degree-day5, bio2, bio8, bio9, bio17, bio19	7	16	4024.5	0.0	1	0.778	0.15
MaxEnt_EnvDef (Default settings)	Degree-day8.3, degree-day5, bio2, bio8, bio9, bio17, bio19	7	53	4153.5	129.0	3	0.765	0.17
MaxEnt_EnvClimex	Degree-day8.3, degree-day5, bio2, bio8, bio9, bio17, bio19, Climex_EI	8	29	4037.6	13.1	2	0.770	0.16
MaxEnt_Climex	Climex_EI, Climex_HS	2	5	4378.2	353.7	4	0.681	0.09

AIC_c is the Akaike's Information Criterion corrected for small sample size; AUC is area under the ROC curve; Climex_EI and Climex_HS are EI and heat stress index generated by CLIMEX model, respectively. All correlations were significant ($P < 0.0001$). MaxEnt_Env is MaxEnt model with only environmental variables; MaxEnt_EnvDef is MaxEnt_Env with default settings; MaxEnt_Climex is model with only CLIMEX outputs.

trap captures) at 573 ± 19.0 DD (mean \pm SE) in Utah and 592 ± 42.1 DD in Washington. Jones et al. (1991) and Song et al. (2003) detected last adult spring emergence between 1700 and 1800 DD at various locations in Utah and Oregon (The Dalles and Hood River).

Temperature Index. The lower temperature threshold for growth (DV0) was set at 3°C (van Kirk and AliNiazee 1982), as diapause development rate of *R. indifferens* pupae after exposure to different cold temperatures was optimum at 3°C. Lower optimum temperature for growth (DV1) was set at 5°C (Frick et al. 1954, van Kirk and AliNiazee 1981). The upper optimum temperature for growth (DV2) and the upper temperature threshold for growth (DV3) were set at 25 and 28°C, respectively (Stark and AliNiazee 1982).

Moisture Index. The soil moisture (SM) index in CLIMEX model was used as a proxy for moisture availability. A hydrological model that uses rainfall and evapotranspiration was used to calculate the weekly soil moisture balance for determining population growth. A value of SM = 0 indicates no soil moisture; SM = 0.5 indicates soil moisture content is 50% of field capacity; SM = 1 indicates that the soil moisture content is 100% of capacity; and SM > 1.0 indicates the possibility of excessive amounts of rainfall and soil moisture (Sutherst et al. 2007). The initial soil moisture parameters for *R. indifferens* (SM0, SM1, SM2, and SM3; Table 1) were set based on Yee (2013), and the values were iteratively adjusted to fit the known distribution of the fly.

Stress Indices. Temperature threshold for cold stress (TTCS) was set at -6°C (van Kirk and AliNiazee 1982), as diapause development was slow at 0 and -3°C. The cold stress affected *R. indifferens* distribution in southern parts of British Columbia, Canada. The cold stress accumulation rate (THCS) was set to -0.001 wk^{-1} to fit the fly's distribution in British Columbia. Heat stress likely affects the distribution of *R. indifferens* in the southwestern United States. The temperature threshold for the heat stress was set 28°C because the upper threshold is close to 30°C (Jones et al. 1991). The heat stress accumulation rate (THHS) was set to 0.009 wk^{-1} to match the fly's current known distribution in the southwestern United States.

The soil moisture threshold for dry stress (SMDS) and dry stress accumulation rate (HDS) may constrain the fly's distribution in southeastern parts of California

and southern Arizona and New Mexico. These parameters were iteratively adjusted to match the fly's absence from these areas. High soil moisture appears to limit the distribution of *R. indifferens* in the Olympic Peninsula in western Washington, Vancouver Island, and the coastal areas of western Canada. Therefore, wet stress parameters were adjusted accordingly to ensure absence of the fly from these areas.

Results

Model Selection and Model Performance. The MaxEnt model with seven environmental variables (MaxEnt_Env) had the lowest AIC_c value and was ranked first among evaluated models (Table 2). This model was fitted with simpler settings (only linear, quadratic, and product features) and a regularization parameter value of 1; the default settings in MaxEnt resulted in a relatively lower accuracy model (MaxEnt_EnvDef) with a large number of parameters (Table 2) and nonsensical response curves. The model with only CLIMEX layers (MaxEnt_Climex) as input variables performed worse. All models performed better than random with AUC_{cv} > 0.50 (Table 2).

Both CLIMEX and MaxEnt models performed well when tested using 20% withheld data (Table 3). The MaxEnt_Env model tested the best, with the highest partial AUC ratio of 1.87 (± 0.03) and very low omission rates (Table 3). The CLIMEX model correctly predicted 81% of the withheld test data points and 82% of all *R. indifferens* occurrence records (Table 3).

Potential Distribution of *R. indifferens* in Western North America and Eight Countries. Results from both niche models conformed well to the current known distribution of *R. indifferens* in western North America (Fig. 1). The MaxEnt model predicted high climatic suitability for *R. indifferens* in central and northeastern parts of Washington, western Oregon, northern California and the Sierra Nevada Mountains, northcentral Utah, northwestern Montana, western Colorado, central New Mexico, and central parts of southern British Columbia (Fig. 1a). The CLIMEX model also predicted closely matching suitable areas for *R. indifferens* but differed most in Montana, Wyoming, and Oregon (Fig. 1a and b).

The models predicted climatically suitable areas for *R. indifferens* in high altitude areas of the Andean

Table 3. Summary of *R. indifferens* model validation using AUC and sensitivity metrics

Model (trained using 80% of the data; $n = 147$)	AUC _{MaxEnt}		pAUC (\pm SD)		Sensitivity using 20% withheld data ($n = 37$) from western North America		
	20% withheld data from western North America ($n = 37$)	20% withheld data from western North America ($n = 37$)	0% training omission rate or LPT	2% training omission rate	5% training omission rate		
MaxEnt_Env	0.795	1.87 (\pm 0.03)	1.0	0.97	0.97		
MaxEnt_Env (Default settings)	0.797	1.84 (\pm 0.05)	0.97	0.92	0.92		
MaxEnt_EnvClimex	0.784	1.85 (\pm 0.04)	1.0	0.97	0.87		
MaxEnt_Climex	0.635	1.62 (\pm 0.10)	1.0	0.92	0.92		
CLIMEX only ^a	-	-	0.81 for 20% Test data (0.82 for all data)				

AUC is area under the ROC curve calculated by MaxEnt; pAUC is the partial AUC ratio statistic (Peterson et al. 2008). Sensitivity is the percentage of correctly predicted presences and varies from 0 to 1.0; a value of 1.0 indicates 100% correctly predicted presences (i.e. higher accuracy). LPT is lowest predicted threshold; 2% training omission means that two percent of training locations (i.e. *R. indifferens* presences) fell outside the predicted suitable area.

^a Training omission rates do not apply to CLIMEX model and locations with $EI \geq 0$ were interpreted as correctly predicted presences.

range in Colombia and western Venezuela, northern and northeastern parts of India, central Taiwan, and parts of Vietnam. The models predicted no suitable habitat for *R. indifferens* in Indonesia, Malaysia, and Thailand (Fig. 1a and b, and Fig. 2a and b).

Factors Influencing Establishment of *R. indifferens*. Precipitation of the driest quarter and degree-days at average temperature $\geq 8.3^\circ\text{C}$ were the strongest predictors of *R. indifferens* probability of presence in the MaxEnt_Env model, with average percent contributions of 30 and 21, respectively (Table 4).

Heat stress limited the distribution of *R. indifferens* in southern parts of North America, the majority of

Colombia and Venezuela, southern India, Indonesia and Malaysia, western Taiwan, Thailand, and Vietnam (Fig. 3a). Cold stress limited the distribution in very high altitude areas of the Rocky Mountains, northern parts of western North America, and northern India (Fig. 3b). Wet stress limited the distribution in the southern parts of Colombia and Venezuela, Indonesia and Malaysia, and eastern Taiwan (Fig. 3c)

A detailed analysis for chilling requirement using NAPPFAST showed no suitable areas for *R. indifferens* in a majority of Colombia, all of Venezuela, Indonesia, Malaysia Taiwan, Thailand and Vietnam, and southern India (Figs. 1c and 2c).

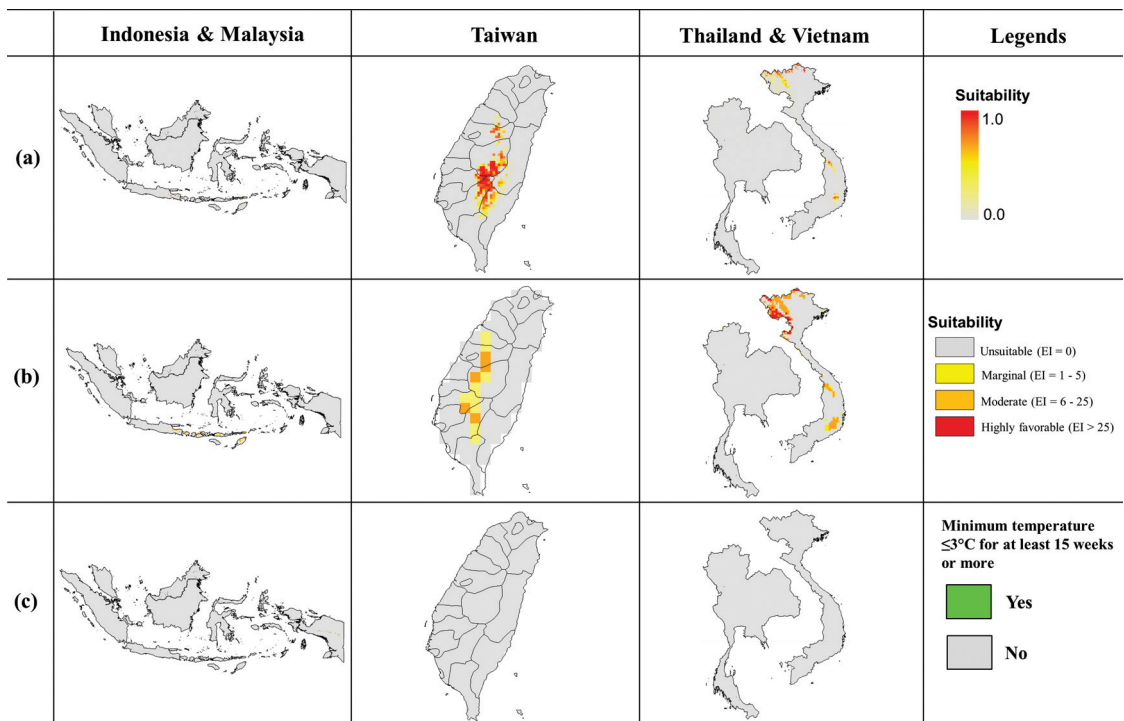


Fig. 2. Projected potential distribution or climatic suitability for *R. indifferens* in Indonesia and Malaysia, Taiwan, and Thailand and Vietnam using (a) MaxEnt, (b) CLIMEX; and (c) chilling requirement map for *R. indifferens* (minimum temperature $\leq 3^\circ\text{C}$ for ≥ 15 wk) using NAPPFAST.

Table 4. Average percent contribution of environmental variables to different MaxEnt models

Variable	MaxEnt_Env	MaxEnt_EnvDef	MaxEnt_EnvClimex	MaxEnt_Climex
Precipitation of driest quarter (Bio17; mm)	29.8	18.9	16.0	–
Degree-days with avg temperatures $\geq 8.3^{\circ}\text{C}$	20.8	22.3	11.8	–
Mean diurnal range in temp (Bio2; $^{\circ}\text{C}$)	19.8	12.9	7.4	–
Precipitation of coldest quarter (Bio19; mm)	11.8	13.5	21.5	–
Degree-days with avg temperatures $\leq 5^{\circ}\text{C}$	10.5	25.7	7.6	–
Mean temp of wettest quarter (Bio8; $^{\circ}\text{C}$)	4.1	2.4	9.0	–
Mean temp of driest quarter (Bio9; $^{\circ}\text{C}$)	3.1	4.5	2.8	–
CLIMEX EI	–	–	23.9	58.6
CLIMEX heat stress index	–	–	–	41.4

Values were averaged across 10 replicate runs.

Most of the eight countries did not have any of the 15 host plant species for *R. indifferens*, with the exception of northern India, which had sweet cherry (*P. avium*), sour cherry (*P. cerasus*), cherry plum (*P. cerasifera*), and apricot (*P. armeniaca*; Fig. 4).

Discussion

Both niche models, MaxEnt and CLIMEX, were successful in capturing the current known distribution of *R. indifferens* in western North America. The MaxEnt model with climatic variables alone was slightly more accurate than the model with only CLIMEX variables (i.e., EI and heat stress index; Tables 2 and 3). In the native range, all areas where *R. indifferens* currently occurs were accurately predicted as being climatically suitable, with chilling requirements being met, and having suitable host plant species (Figs. 1 and 4). Model projections for the eight countries from both MaxEnt and CLIMEX models matched closely (Figs. 1 and 2), which might be explained because MaxEnt included species physiological tolerance variables such as opti-

mum temperature thresholds for *R. indifferens*. These results support Franklin (2013), who suggested that extrapolations from the correlative models into novel environments might improve by considering species-specific functional responses and physiological tolerances.

Overall results suggest no risk of establishment of *R. indifferens* in Colombia, Indonesia, Malaysia, Taiwan, Thailand, Venezuela, and Vietnam based on the optimum chilling requirement for *R. indifferens* needed to successfully break diapause. Furthermore, none of these countries has plants identified as hosts for *R. indifferens*. In contrast, northern parts of India seem to have a higher risk of establishment of *R. indifferens* because the areas are predicted to be climatically suitable, with appropriate chilling requirements, and have four of the host plant species for the fly. Higher heat stress or wet stress significantly lowered the risk of establishment of *R. indifferens* in the eight tropical countries (Fig. 3).

Host Plant Distributions and Chilling Requirements. Both MaxEnt and CLIMEX models predicted only climatic suitability of different areas for *R. indifferens*; neither of them included presence of host plant

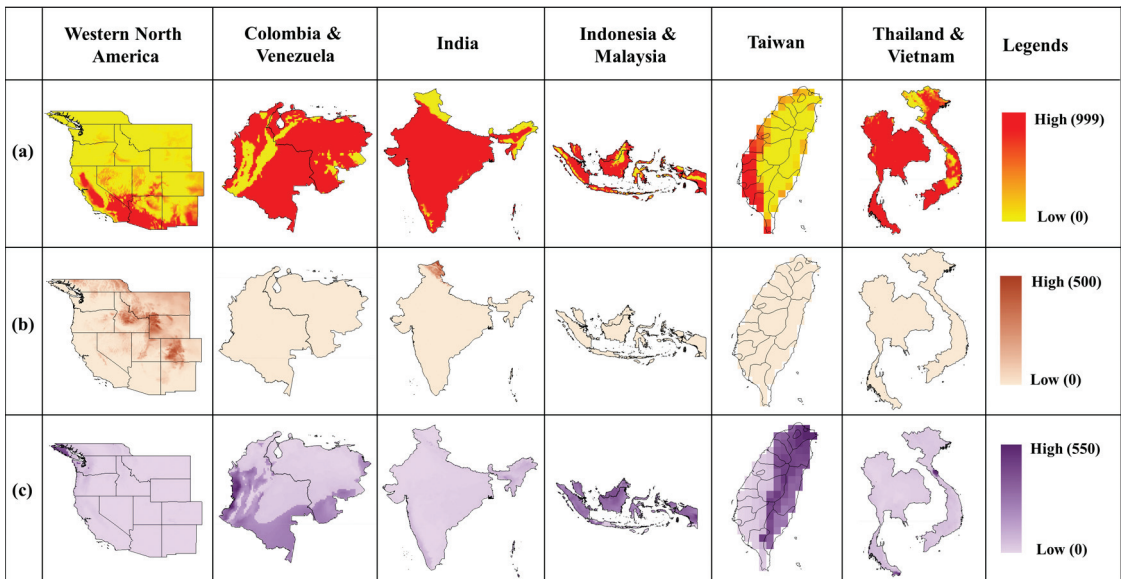


Fig. 3. Temperature and moisture stresses on potential distribution of *R. indifferens* in western North America and eight countries of quarantine concern—(a) Heat Stress Index, (b) Cold Stress Index, and (c) Wet Stress Index. Darker colors represent high stress and lighter colors represent low stress.

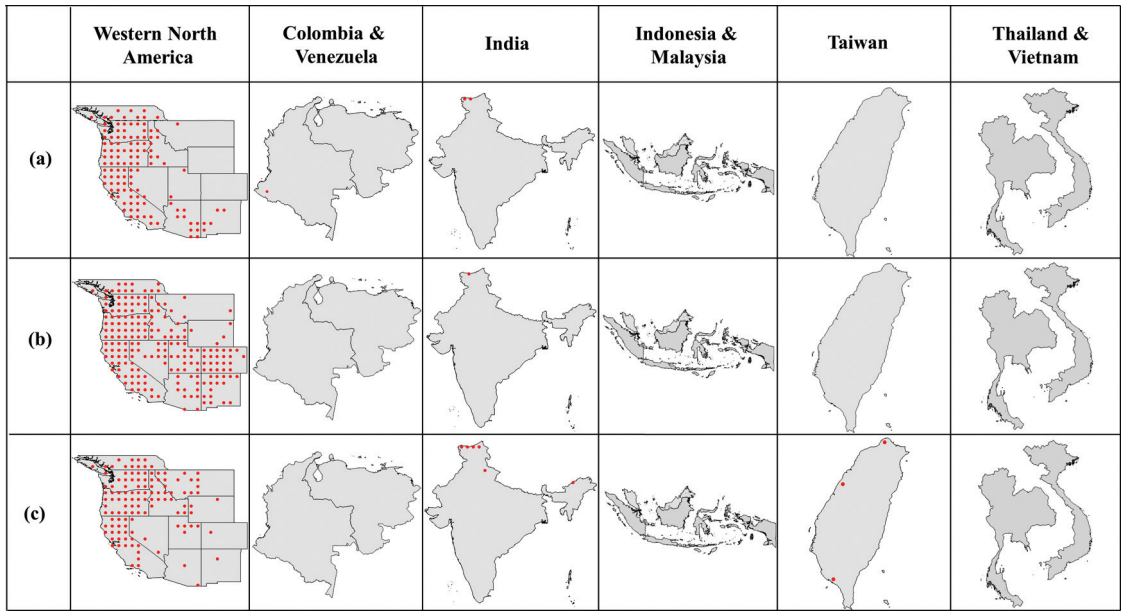


Fig. 4. Distribution of *R. indifferens* host plant species in different countries. (a) Major hosts: 1) sweet cherry, *P. avium*, 2) sour cherry, *P. cerasus*, 3) bitter cherry, *P. emarginata*, 4) mahaleb cherry, *P. mahaleb*, 5) bird cherry, *P. padus*; (b) minor or rare hosts: 1) choke cherry, *P. virginiana*, 2) pin cherry, *P. pensylvanica*, 3) cherry Laurel, *P. laurocerasus*, 4) cherry Plum, *P. cerasifera*, 5) cascara, *Rh. purshiana*; and (c) Incidental hosts: 1) apricot, *P. armeniaca*, 2) black hawthorn, *C. douglasii*, 3) Japanese plum, *P. salicina*, 4) Pacific plum, *P. subcordata*, 5) Chinese crabapple, *M. spectabilis*.

species, natural enemies, and other factors that may be responsible for limiting the actual distribution and establishment of insect pests (Sutherst et al. 2007). Presence of host plant species is one of the essential requirements for insect plant pests to establish in a new region (Bacon et al. 2014). In the absence of suitable host species insects cannot complete their life cycles. *R. indifferens* females lay eggs in the host plants' fruits, eggs develop into larvae, feed on the fruit, exit the fruit and pupate in the soil, and after a significant diapause period, emerge as adults (Frick et al. 1954). Therefore, even if certain areas are predicted to be climatically suitable for *R. indifferens*, its survival and establishment would be highly unlikely in the absence of host plant species. In addition, average climatic conditions (e.g., average temperature and moisture) are not adequate, as sufficient chilling degree-days required to break the diapause of most individuals are also required. For example, the Central Valley of California in the United States has host plant species for *R. indifferens*, but the chilling requirement is not met, so the pest cannot establish there. The occurrence of *R. indifferens* in the Central Valley of California has never been reported, most probably owing to heat stress (Kumar et al. unpublished data). Furthermore, CLIMEX predicted climatic suitability in several areas in Wyoming (Fig. 1a and b), as they also meet the chilling requirement (Fig. 1c). However, *R. indifferens* has never been reported from there for unknown reasons, either because the fly has not spread there or it has simply not yet been reported.

Model Limitations and Uncertainties. Uncertainties in niche models might arise from several different

sources, including spatial error, sampling bias and incompleteness of occurrence data, sample size, multicollinearity among predictors, choice of predictors, spatial resolution of predictors, spatial autocorrelation, modeling techniques and calibration settings, species characteristics, and extent of the study area (Guisan et al. 2007a,b; Taylor and Kumar 2012; Anderson 2013; Dormann et al. 2013; Syfert et al. 2013). Correlative niche models, especially presence-only and presence-background (e.g., MaxEnt), are also affected by the way background extent is defined (Phillips 2008, Phillips et al. 2009, VanDerWal et al. 2009). Here, some of these uncertainties were addressed by 1) using more than one niche model, 2) reducing the number of variables by assessing cross-correlations, 3) examining spatial autocorrelation and sampling bias before modeling, 4) using "fade-by-clamping" in MaxEnt to avoid erroneous extrapolations, 5) including species-specific phenology variables to represent species characteristics, and 6) drawing background points using a KDE surface.

Propagule pressure is another important determinant of whether a nonnative insect pest would become established in a novel area (Bacon et al. 2014). Therefore, future niche models of *R. indifferens* should consider propagule pressure in addition to host availability, climatic suitability, and chilling requirement. Propagule pressure varies at different ports of entry, so even if certain areas in a country (e.g., northern India) meet other requirements for a species, they may not receive any propagules if the commodities or fruits enter from a different port in unsuitable regions (e.g., Mumbai and Chennai ports in southern India). In-

cluding propagule pressure using trade volume in correlative or mechanistic niche models (e.g., MaxEnt, CLIMEX) is currently a daunting task or impossible (e.g., NAPPFAST). Combining niche model predictions with traditional pest risk assessments using @Risk probabilistic modeling software (Palisade Corporation, New York, NY) that can include propagule pressure might result in improved assessment of the potential for pest introduction and establishment.

Climatic Data Limitations for Pest Risk Analyses. The most commonly used climatic dataset, WorldClim (Hijmans et al. 2005), and the recently developed CliMond dataset (Kriticos et al. 2012) may not be adequate to correctly assess the risk of establishment of insect plant pests, especially for insects that have critical temperature or moisture threshold requirements. For example, the optimal chilling requirement for *R. indifferens* was not adequately incorporated into MaxEnt and CLIMEX models because they are composed of older average monthly, and weekly temperature data, respectively. We had to augment our analyses by using the NAPPFAST system to incorporate the optimal chilling requirement because it had the most up-to-date daily temperature records from numerous weather stations around the globe. Both WorldClim and CliMond datasets are centered on 1975 and are not concurrent with some of the *R. indifferens* distributional records from western North America. This mismatch may have affected the projected distribution of climatically suitable areas for *R. indifferens* in its native range and the eight tropical countries.

Trade Implications and Quarantine Management. The modeling and analyses presented here along with the best available scientific information should be useful to U.S. trading partners in determining the potential for introduction and establishment of *R. indifferens*. In some cases existing fruit importation policies and quarantine regulations and trade barriers may be based on decades-old information (e.g., Willett et al. 2009; Neven 2012, 2013). Imports of fresh U.S. sweet cherries from the Pacific Northwest by countries that do not have climatically suitable areas, do not meet the optimal chilling requirement for *R. indifferens*, and have no host plant species, should not be of significant risk for the establishment and spread of *R. indifferens*. For example, the current quarantine regulations in Indonesia, requiring cold treatment or fumigation for sweet cherries imports to control fruit flies (NHC 2011) appear to be overly restrictive on a number of levels. Given our results, such rules should be reevaluated and quarantine restrictions amended.

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