

Assessing the Global Risk of Establishment of *Cydia pomonella* (Lepidoptera: Tortricidae) using CLIMEX and MaxEnt Niche Models

SUNIL KUMAR,^{1,2} LISA G. NEVEN,³ HONGYU ZHU,⁴ AND RUNZHI ZHANG⁴

J. Econ. Entomol. 108(4): 1708–1719 (2015); DOI: 10.1093/jee/tov166

ABSTRACT Accurate assessment of insect pest establishment risk is needed by national plant protection organizations to negotiate international trade of horticultural commodities that can potentially carry the pests and result in inadvertent introductions in the importing countries. We used mechanistic and correlative niche models to quantify and map the global patterns of the potential for establishment of codling moth (*Cydia pomonella* L.), a major pest of apples, peaches, pears, and other pome and stone fruits, and a quarantine pest in countries where it currently does not occur. The mechanistic model CLIMEX was calibrated using species-specific physiological tolerance thresholds, whereas the correlative model MaxEnt used species occurrences and climatic spatial data. Projected potential distribution from both models conformed well to the current known distribution of codling moth. None of the models predicted suitable environmental conditions in countries located between 20°N and 20°S potentially because of shorter photoperiod, and lack of chilling requirement (<60 d at ≤10°C) in these areas for codling moth to break diapause. Models predicted suitable conditions in South Korea and Japan where codling moth currently does not occur but where its preferred host species (i.e., apple) is present. Average annual temperature and latitude were the main environmental variables associated with codling moth distribution at global level. The predictive models developed in this study present the global risk of establishment of codling moth, and can be used for monitoring potential introductions of codling moth in different countries and by policy makers and trade negotiators in making science-based decisions.

KEY WORDS biosecurity, species distribution modeling, pest risk analysis, insect pest, quarantine pest

The codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), is one of the most destructive and economically important fruit pests of apples, its preferred host, as well as walnuts, pears, apricots, and plums in most fruit-growing temperate regions of the world (Barnes 1991, Beers et al. 1993, Neven 2012). It is a pest of quarantine concern in several countries and regions where it currently does not occur (e.g., Colombia, Japan, South Korea, and Chinese Taiwan). Codling moth has the potential to cause 100% infestation in untreated apple orchards (Beers et al. 2003). Other tree fruits such as pears (*Pyrus* spp.) and walnuts are less susceptible to codling moth infestation (Barnes 1991). Codling moth is considered to have originated somewhere in eastern Eurasia and was inadvertently introduced across the world through infested fruits (Lloyd 1960); it was introduced to North America around 1750 (Slingerland 1898).

Codling moth is an internal feeding pest and its biology is very well-studied because of its high economic importance (Neven et al. 2000, Neven 2012). It is a multivoltine species with a facultative diapause, and has the ability to adapt to diverse climatic conditions. This pest has one to five generations per year with fewer generations further away from the equator (Anonymous 2014a). *C. pomonella* has five larval instars and overwinters under the tree bark or at the base of the tree as fifth-instar diapausing larvae (Weitzner and Whalon 1987). Diapause is triggered primarily by shorter day lengths in late summer (Riedl 1983; Neven 2012, 2013). The critical photoperiod (i.e., the day length at which ≥50% of the population enters diapause) for codling moth varies from 13.5 to 15.5 h of day light (Shel'deshova 1967, Anonymous 2014b). *C. pomonella* also has chilling requirement of <60 d at ≤10°C temperature to break diapause (Neven 2013).

International trade of fruits, packing materials, and other commodities (e.g., seeds and plant parts) can potentially carry pests and cause inadvertent introductions in importing countries where the pest is not established. Therefore, the World Trade Organization (WTO) requires its members to establish national Sanitary and Phytosanitary Measures (SPS; WTO 2014) measures consistent with international standards (WTO 2014). The plants, insects, and disease pathogens

¹ Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499.

² Corresponding author, e-mail: Sunil.Kumar@colostate.edu.

³ United States Department of Agriculture- Agriculture Research Service, Yakima Agricultural Research Laboratory, 5230 Konnowac Pass Rd., Wapato, WA 9895.

⁴ Institute of Zoology, Chinese Academy of Sciences, Beichen West Rd., Chaoyang, Beijing 100101, China.

regulated under SPS measures cost ~US\$80 billion to the U.S. economy (Pimentel et al. 2000). Most often information on the establishment potential of a quarantine pest for the importing countries is insufficient to develop biologically and ecologically accurate pest risk analyses; countries impose quarantine measures simply based on host species' presence (Willett et al. 2009). Therefore, assessment of the potential risk of establishment of pest species such as codling moth in the importing countries can be a valuable tool for trading partners' national plant protection and quarantine officers, and policy makers in designing import/export rules and regulations, and negotiating trade. Existing phytosanitary restrictions may be eased or re-evaluated if the suitable environmental conditions do or do not exist in the importing countries.

Climate is one of the most important determinants of the distribution of phytophagous insects and their host plants and natural enemies (Kiritani 2006, Tuda et al. 2006). Ecological niche models (ENMs) can be used to quantify and map the bioclimatic potential of insect pests and their host plants. ENMs are increasingly being used for assessing the potential for establishment of insect pests and other species of concern (Rafoss and Saethre 2003; Li et al. 2009; De Meyer et al. 2010; Evangelista et al. 2011; Lozier and Mills 2011; Kriticos et al. 2012a; Kumar et al. 2014a,b,c). These models can be built using either physiological information from experimental laboratory or field studies (mechanistic models) or by integrating species occurrences (presence and presence-absence or abundance) with spatial environmental variables of the study area (correlative models). The mechanistic ENMs include processes that are directly related to fundamental niche of the species, whereas the correlative ENMs model species-environment relationship in the study area (Elith 2015). The correlative models, if not fitted appropriately, may not perform well when projected to novel environments (Webber et al. 2011, Owens et al. 2013). However, recent studies have shown that predictive performance of these models, when projected to novel environments can be significantly improved if they are fitted with hypothesis-driven, biologically meaningful variables with moderate level of complexity (Kumar et al. 2014a,b). Both types of niche models have their advantages and disadvantages (Dormann et al. 2012).

Despite the high economic importance of codling moth to fruit growers worldwide, global establishment risk maps for codling moth are not available except a few regional studies (e.g., Yang (2008), and Liang et al. (2010) for China; and Rafoss and Saethre (2003) for Norway). Our objectives were to 1) assess the global potential risk of establishment of codling moth using two different ENMs, and 2) identify environmental drivers associated with codling moth potential distribution.

Materials and Methods

Occurrence Data. Species presence data (i.e., sites where codling moth occurred) were collected from

published articles, books, reports, and online databases (Supp Table 1 [online only]). We also digitized apple orchard locations in the United States and other countries where codling moth is known to occur, and used these as potential codling moth presence locations (Beers et al. 2003, Knight 2008), except Japan and South Korea. The county-level codling moth occurrence records for the continental United States reported by National Agricultural Pest Information System (NAPIS; <http://pest.ceris.purdue.edu/index.php>) were replaced by apple orchard coordinates. The Google Earth (<https://www.google.com/earth/>) and the Google Maps (<https://www.google.com/maps/preview>) with the satellite imagery in the background were used to locate apple orchards where codling moth was reported to occur in cases where exact geographic coordinates were not available from the published studies. *C. pomonella* occurrence data from China were collected from the old reports and the National Information Distribution of Quarantine Pests issued by the Chinese Department of Agriculture in 1996. Some of the infested locations occurring between 1987 and 2005 were provided by the Provincial Plant Protection and Quarantine Services. Data from 2005 to 2012 were obtained from the National Codling Moth Monitoring Workshop reviews. In total, 1,055 occurrence records from 35 countries across the world were collected. These records were reduced to 971 after removing duplicates and applying "spatial filtering" using SDMToolbox (Brown 2014; <http://sdmtoolbox.org/>) to reduce spatial autocorrelation; filtered occurrence data points were >10 km apart (Veloz 2009, Boria et al. 2014). This distance is higher than the maximum dispersal distance (8 km) reported for male codling moth in experiments conducted by Mani and Wildbolz (1977), in which the majority of individuals (90%) were recaptured within 1 km from the release point.

Niche Modeling. From a large suite of available correlative and mechanistic niche models (Franklin 2009, Peterson et al. 2011), we selected two commonly used models—MaxEnt and CLIMEX. These models have been found very effective in predicting insect pests' establishment risk (Lozier and Mills 2011; Kriticos et al. 2012a; Kumar et al. 2014a,b,c).

MaxEnt Niche Model. Our first niche model was a correlative maximum entropy-based model or MaxEnt (version 3.3.3k; Phillips et al. 2006, Elith et al. 2011). We chose the MaxEnt model because it is a presence-background model, making it most suitable for our codling moth occurrence data; absence data at global scale for codling moth were not available. The MaxEnt model has been widely used in modeling potential distributions of insect pests (Evangelista et al. 2011; Lozier and Mills 2011; Kumar et al. 2014a,b,c) and other species of concern (Kumar et al. 2009, Li et al. 2009, De Meyer et al. 2010, Evangelista et al. 2011). MaxEnt integrates species occurrences with background data (i.e., randomly selected points) from spatial environmental variables representing different environmental gradients in the study area and generates probability of species' presence (Phillips et al. 2006). It identifies areas that have conditions most similar to species'

current known occurrences and ranks them from 0 (unsuitable or most dissimilar) to 1 (most suitable or most similar). MaxEnt generates a set of feature classes (i.e., linear [L], quadratic [Q], product [P], threshold [T], and hinge [H]) using environmental variables. It uses a regularization multiplier (RM) to reduce the number of parameters and thus automatically controls the model complexity (Phillips and Dudik 2008, Elith et al. 2011). The default RM value is 1; a smaller value of RM (≤ 1) may potentially overfit the model and produce more restricted distribution whereas a higher value (> 1) would result in simpler models with less discriminating power and broader species potential distribution (Phillips et al. 2006). Therefore, tuning of MaxEnt model settings has been suggested for selecting an optimal model to enhance predictions (Shcheglovitova and Anderson 2013, Boria et al. 2014).

Environmental Data Layers. Nineteen bioclimatic variables' data layers were acquired from the WorldClim dataset (Hijmans et al. 2005; <http://www.worldclim.org/>) at 2.5 arc-minutes spatial resolution (~ 4.5 km). These bioclimatic variables were generated using monthly temperature and precipitation data averaged over a period from ~ 1950 to 2000, and represent average temperature and precipitation, seasonal variables, and climatic extreme indices (Hijmans et al. 2005). These variables were chosen based on their potential biological relevance to codling moth and their use in previous insect pest niche modeling studies (e.g., Evangelista et al. 2011; Lozier and Mills 2011; Kumar et al. 2014a,b). Earlier studies have shown that including species-specific phenology variables improved the correlative niche model predictions (Sambaraju et al. 2012; Kumar et al. 2014a,b). Therefore, we also considered "degree days at average temperature $> 10^{\circ}\text{C}$ " as a potential predictor in niche models because 10°C is the lower temperature threshold for development of codling moth populations (Shel'deshova 1967); it was calculated in Arc Map (Environmental Systems Research Institute [ESRI] 2013) using monthly temperature data layers. A latitude layer was also included as one of the environmental variables because it is often used as a surrogate for length of daylight because the number of daylight hours varies with latitude and day of the year (Enquist and Niklas 2001, Jetz et al. 2008, Dadvand et al. 2011). For example; a 10° shift in latitude to the North resulted in an increase of 1.25 h in the critical photoperiod (Riedl and Croft 1978). The length of daylight has an immense influence on codling moth diapause and overall physiology (Shel'deshova 1967; Riedl and Croft 1978; Riedl 1983; Willett et al. 2009; Neven 2012; 2013). Latitude was an important predictor of codling moth average first spring emergence in North America (Jones et al. 2013). Thus, we utilized latitude to represent day length and WorldClim bioclimatic variables to represent climate-driven environmental conditions.

Variable Selection, Model Settings, and Model Evaluation and Validation. All environmental variables were examined for cross-correlation (Pearson correlation coefficient, r) and highly correlated variables ($|r| > 0.75$) were dropped (Supp Table 2 [online only])

to account for multicollinearity (Dormann et al. 2013). The decision to drop or retain a variable was based on its biological relevance to codling moth, its relative predictive power, and ease of interpretation. Latitude was not dropped even if it had high correlation with mean annual temperature (bio1; $r = 0.93$) because of its greater indirect influence on codling moth diapause. The total number of variables considered in MaxEnt model was reduced to 10 of 21.

A bias surface for MaxEnt models was generated using SDMToolbox to account for potential sampling bias in the occurrence data because bias in the data can negatively affect niche models' performance (Phillips 2008, Syfert et al. 2013). Fifty thousand random background points were automatically drawn by MaxEnt from all terrestrial areas of the world; the background extent was defined based on the biotic-abiotic-mobility framework suggested by Soberon and Peterson (2005). The "fade-by-clamping" procedure was used to avoid extrapolations beyond the environmental range of the training data (Owens et al. 2013). The percent contributions of different variables and jackknife features in MaxEnt were used to examine relative importance of different environmental predictors.

Initial MaxEnt model was run with default settings, and later, overfitting experiments were conducted with different combinations of feature classes (e.g., LQP, LQPH, and LQPTH) and RM values (ranging from 1 to 3). The complex model generally resulted in very complex and biologically nonsensical response curves, and were discarded (Fig. A3; Kumar et al. 2014b). The optimal model with eight predictor variables was selected using the Bayesian information criterion (BIC) calculated using ENMTools (Warren et al. 2010). We used BIC for model selection instead of Akaike's information criterion (AIC) because BIC has higher penalty for model complexity than AIC.

Performance of MaxEnt models was evaluated using threshold-dependent and threshold-independent metrics. MaxEnt generated area under the receiver operating characteristic (ROC) curve (AUC; Phillips et al. 2006) and partial AUC ratio (pAUC; Peterson et al. 2008) were used as threshold independent measures of model performance. The AUC values vary from 0 to 1; 0.5 shows model performance not better than random, values < 0.5 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). The 10-fold cross-validation procedure in MaxEnt was used and averaged test AUC values (AUC_{cv}) across the 10 replicates were reported. Partial AUC ratio (pAUC) values were calculated by splitting the data into training (80%) and test (20%) sets using a Visual Basic program (Barve, 2008). A pAUC value of > 1.0 shows better performing model. In addition, two threshold-dependent metrics were used: omission rate (OR) at minimum training presence threshold or lowest predicted threshold (LPT; Pearson et al. 2007), and omission rate at 10% training presence threshold. The expected value of test omission rate at LPT is 0, whereas at 10% training presence threshold it is 0.10; higher than expected

omission rates show poor performance of the models (Boria et al. 2014).

CLIMEX Niche Model. Our second niche model was a semi-mechanistic model CLIMEX (version 3.0), which has been widely used in hundreds of studies on pest risk assessment and climate change (Sutherst et al. 2007; Kriticos et al. 2012a; Kumar et al. 2014a,b). CLIMEX uses an integrative inductive–deductive approach based on species' physiological tolerances, climatic data, and species known distribution to estimate climatic suitability for a species (Sutherst and Maywald 1985; Sutherst et al. 2007; Ireland et al. 2013). The simulation model from CLIMEX produces an index called Ecoclimatic Index (EI), an index of climatic suitability for a species that varies from 0 to 100 (0 represents unsuitable [no population growth] and 100 optimal conditions). The EI is a combination of Growth Index and Stress Indices; the Growth Index describes the potential population growth and development during favorable seasons using temperature, moisture, radiation, substrate, light, and diapause indices, and stress indices (cold, hot, dry, and wet stresses) describe the limitations to population growth and species distribution due to different stresses (Sutherst et al. 2007). The “Compare Locations” function in CLIMEX was used to develop a simulation model to estimate climatic suitability for the establishment for codling moth. The CliMond CM10_1975H_V1 climatic dataset (Kriticos et al. 2012b; available at <http://www.climond.org>) interpolated at 10 arc minute (~18 km) resolution was used in CLIMEX modeling. This dataset has long-term monthly climate means centered on year 1975 for precipitation, maximum temperature, minimum temperature, and relative humidity at 9 a.m. and 3 p.m.

Values for CLIMEX model parameters were defined based on published laboratory studies and phenological observations on physiological tolerances of codling moth. Initial parameter values were taken from CLIMEX User's Guide (Sutherst et al. 2007) and Rafoss and Saethre (2003), and were modified based on results from recently conducted experiments and species' current known distribution (Table 1). The lower temperature threshold for growth (DV0) was set at 9°C, based on Howell and Neven (2000), Saethre and Hofsvang (2002), and Rafoss and Saethre (2003). Earlier studies suggested DV0 to be close to 10°C (Shel'deshova 1967), a commonly used temperature threshold in most degree-day models (e.g., Riedl and Croft 1978, Howell and Neven 2000, Jones et al. 2013); however, setting DV0 to 10°C did not predict codling moth distribution in southern Norway (Rafoss and Saethre 2003), so DV0 was reduced to 9°C. Saethre and Hofsvang (2002) found that the lower egg development temperature for codling moth Norwegian populations is lower (1–2°C) than the 10°C threshold. The lower optimum and upper optimum temperature thresholds (DV1 and DV2) were set to 15 and 27°C, respectively, based on the studies by Shel'deshova (1967), Rock and Shaffer (1983), Howell and Neven (2000), and Blomefield and Giliomee (2011) (Table 1). The upper development temperature threshold, after which species growth stops (DV3), was set to 34.4°C,

based on the studies by Proverbs and Newton (1962), Rock and Shaffer (1983), and Pitcairn et al. (1991). The number of degree-days above DV0 required to complete one generation (PDD) for codling moth was set to 580. The PDD reported in several studies conducted at different latitudes of codling moth distributional range varied from 510–600 (Shel'deshova 1967, Rock and Shaffer 1983, Rafoss and Saethre 2003).

Rainfall and humidity do not have significant effects on codling moth life cycle; however, heavy rainfall may cause larval mortality (Shel'deshova 1967, Anonymous 2014b). Soil moisture threshold values (SM0, SM1, SM2, and SM3) were slightly adjusted from Rafoss and Saethre (2003). We used light index as one of the limiting factors in CLIMEX that was not used in earlier models of codling moth (Sutherst et al. 2007, Rafoss and Saethre 2003). The day length (hours) above which growth is at a maximum (LT0) was set to 15.5 h, while the day length (hours) below which growth is 0 (LT1) was set to 13.5 h, based on studies by Neven (2012, 2013), Stoeckli et al. (2012), and Anonymous (2014c). Diapause index parameters were set based on studies by Shel'deshova (1967), Neven (2012, 2013), Stoeckli et al. (2012), and Anonymous (2014d). Stress parameters were iteratively adjusted from Rafoss and Saethre (2003).

The categorization of EI values is an arbitrary process because these estimated values are species-specific. The EI values were divided into four categories: unsuitable (EI = 0), marginally suitable (EI = 1–5), moderately suitable (EI = 6–25), and highly suitable (EI > 25; Kriticos et al. 2003). CLIMEX model was validated qualitatively by evaluating its ability to predict currently known occurrences of codling moth. Occurrences with EI values > 0 were interpreted as correctly predicted presences.

Results

Model Performance. In total, 12 MaxEnt models, with varying complexity, using different combinations of feature classes and RM were evaluated for predicting codling moth potential distribution (Table 2). All models performed better than random with test AUC_{cv} values ranging from 0.933 to 0.946, and pAUC values from 1.807 to 1.902 (Table 2). All these models also had low omission rates at both lowest predicted threshold (0.001 to 0.004) and 10th percentile training presence threshold (0.100 to 0.144; Table 2). The best model included eight environmental variables, linear, quadratic, product, and threshold (LQPH) features, RM = 2.0, and had the lowest BIC, and low omission rates (Table 2). The lower omission rate represents the better model performance. The simplest model with only one variable (mean annual temperature; bio1) had low omission rates but poor evaluation statistics, highest BIC, and ranked lowest (Model 9; Table 2). The most complex model included 10 variables, LQPTH features, and RM = 1.0, had highest omission rates, and was ranked 9th (Model 10; Table 2). CLIMEX model also performed well and correctly predicted majority of

Table 1. Codling moth parameters for CLIMEX model; initial parameters were obtained from CLIMEX manual (Sutherst et al. 2007) and Rafoss and Saethre (2003) and the values were adjusted by the authors

Parameter		Description	Value
Temperature index (TI)			
DV0		Lower temperature threshold for growth	9°C
DV1		Lower optimum temperature for growth	15°C
DV2		Upper optimum temperature for growth	27°C
DV3		Upper temperature threshold for growth	34.4°C
PDD		Number of degree-days above DV0 needed to complete one generation	580
Moisture index (MI)			
SM0		Lower soil moisture threshold	0.02 ^a
SM1		Lower optimum soil moisture	0.1 ^a
SM2		Upper optimum soil moisture	1.8 ^a
SM3		Upper soil moisture threshold	2.5 ^a
Light index			
LT0		Day length (hours) above which growth is at a maximum	15.5 hr
LT1		Day length (hours) below which growth is zero	13.5 hr
Cold stress (CS)			
TTCS		Temperature threshold for cold stress	−15°C
THCS		Cold stress accumulation rate	−0.0011 week ^{−1}
Heat stress (HS)			
TTHS		Temperature threshold for heat stress	35°C
THHS		Heat stress accumulation rate	0.0001 week ^{−1}
Dry stress (DS)			
SMDS		Soil moisture threshold for dry stress	0.02
HDS		Dry stress accumulation rate	−0.001 week ^{−1}
Wet stress (WS)			
SMWS		Soil moisture threshold for wet stress	2.5
HWS		Wet stress accumulation rate	0.002 week ^{−1}
Diapause index			
DPD0		Diapause induction day length	15
DPT0		Diapause induction temperature	11.0°C
DPT1		Diapause termination temperature	6.0°C
DPD		Diapause development days, defaults to 0, i.e., facultative diapause	90

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

Table 2. Summary of performance statistics and overfitting experiments of codling moth MaxEnt models; the best model is highlighted in Bold

Model no.	Variables	No. of variables	MaxEnt settings		BIC	ABIC	Test AUC _{cv}	pAUC	Omission rate		Model rank
			Features	RM					0%	10%	
1	Bio1, latitude, bio19, bio2, bio7, bio16, elevation, bio15	8	LQPH	2.0	27901.3	0	0.940 (±0.006)	1.893 (±0.02)	0.001	0.110	1
2	Same as above	8	LQPH	1.0	28029.1	127.8	0.943 (±0.004)	1.897 (±0.02)	0.001	0.116	11
3	Same as above	8	LQPH	1.5	27954.7	53.4	0.942 (±0.003)	1.895 (±0.02)	0.001	0.110	8
4	Same as above	8	LQPH	2.5	27931.3	30.0	0.938 (±0.008)	1.890 (±0.02)	0.001	0.108	5
5	Same as above	8	LQP	2.0	27934.9	33.6	0.933 (±0.006)	1.871 (±0.02)	0.001	0.104	6
6	Same as above	8	LQPTH	1.0	28018.8	117.4	0.945 (±0.005)	1.902 (±0.02)	0.002	0.141	10
7	Model1 without elevation	7	LQPH	2.0	27921.6	20.3	0.940 (±0.009)	1.891 (±0.02)	0.001	0.115	4
8	bio1, latitude, bio19, bio2, bio1	4	LQPH	2.0	27948.0	46.7	0.936 (±0.006)	1.883 (±0.02)	0.002	0.109	7
9	bio1	1	LQPH	2.0	28452.3	551.0	0.936 (±0.006)	1.807 (±0.02)	0.001	0.100	12
10	Model1+ bio17, bio18	10	LQPTH	1.0	27987.8	86.5	0.946 (±0.007)	1.900 (±0.02)	0.004	0.144	9
11	Same as above	10	LQPH	2.0	27918.8	17.4	0.942 (±0.004)	1.890 (±0.02)	0.001	0.109	3
12	Same as above	10	LQP	2.0	27915.7	14.4	0.937 (±0.010)	1.881 (±0.02)	0.001	0.112	2

L, Q, P, T and H are linear, quadratic, product, threshold and hinge features, respectively; BIC is Bayesian Information Criterion; RM is regularization multiplier; OR is test omission rate. Test AUC_{cv} is MaxEnt generated 10-fold cross-validation Area Under the ROC Curve; pAUC is partial AUC ratio calculated at 0% omission rate (Peterson et al. 2008).

the currently known occurrences of codling moth and had an omission rate of 0.127.

Potential Distribution of Codling Moth. Projected potential distribution from both models conformed well to the current known distribution of codling moth (Figs. 1 and 2). None of the models predicted suitable environmental conditions in countries between 20th parallels (e.g., Colombia, Ecuador, Peru, and Venezuela in South America). Models predicted suitable conditions in Japan and South Korea where codling moth

currently does not occur but include its preferred host species (i.e., apple). MaxEnt appeared to be slightly overpredicting the potential distribution of codling moth (Fig. 1), whereas CLIMEX seemed to underpredict (Fig. 2). MaxEnt and CLIMEX model predictions remarkably agreed with each other in major codling moth occurrence regions (e.g., North America, Europe, China, India, northern Morocco, northern Algeria, South Africa, southern Australia, Tasmania, New Zealand, central Chile, and Argentina; Figs. 1 and 2).

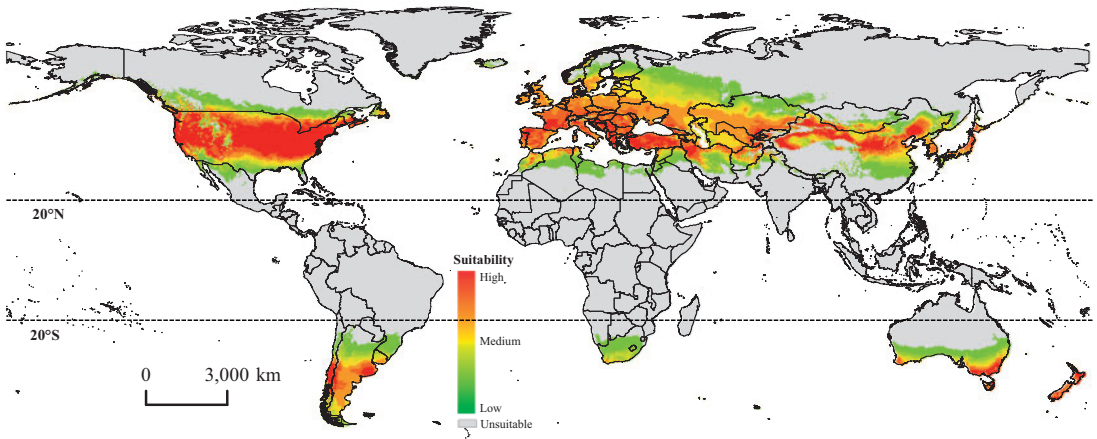


Fig. 1. Global risk of establishment of codling moth using MaxEnt model.

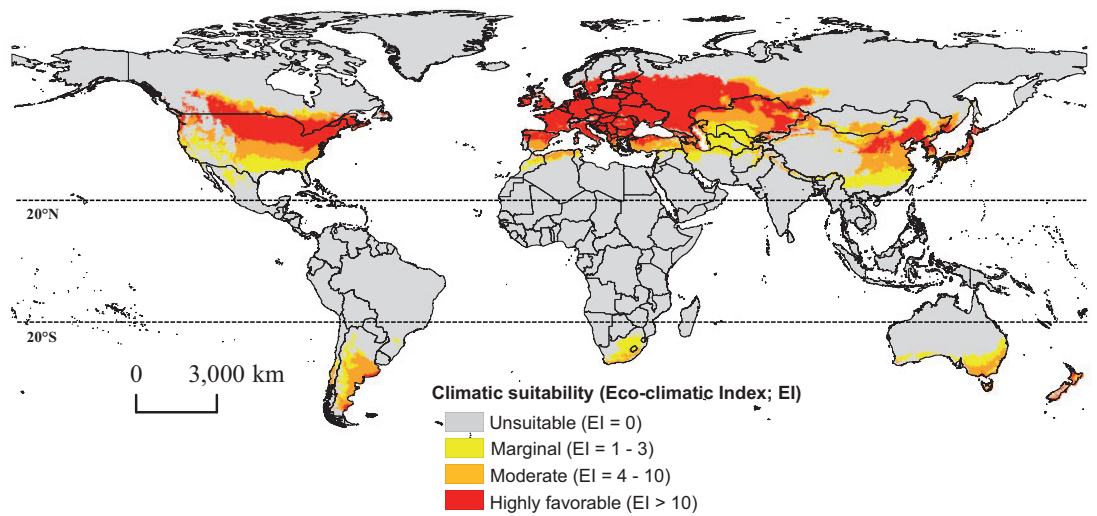


Fig. 2. Global risk of establishment of codling moth using CLIMEX model.

However, both models also differed in some areas. For example, MaxEnt predicted suitable conditions for codling moth in southern Alaska, northern parts of Libya, Egypt, and Saudi Arabia, whereas CLIMEX did not (Figs. 1 and 2). MaxEnt predicted more suitable areas in Xinjiang province in western China than CLIMEX (Figs. 1 and 2; and Supp Fig. 2 [online only]). Enlarged maps depicting more detailed patterns of the potential risk of establishment of codling moth in countries that are current or future potential markets for U.S. grown apples are provided in Supp Figs. 1–5 (online only). None of the models predicted suitable environmental conditions for codling moth in Cambodia, Colombia, Ecuador, southern India, Indonesia, Laos, Malaysia, Peru, Thailand, and Vietnam (Supp Figs. 3–5 [online only]).

Effects of Environmental Factors. Mean annual temperature, latitude (a surrogate for length of day light hours), and precipitation of coldest quarter were

Table 3. Average percent contribution of environmental variables in the best codling moth model; values were averaged across 10 replicate runs

Variable	Percent contribution	Permutation importance
Mean annual temperature (bio1, °C)	64.9	58.7
Latitude (degree decimal)	25.7	28.8
Precipitation of coldest quarter (bio19; mm)	6.0	3.1
Mean diurnal range in temp. (bio2; °C)	2.2	3.4
Precipitation of wettest quarter (bio16; mm)	0.4	2.0
Temperature annual range (bio7; °C)	0.4	2.1
Precipitation seasonality (CV) (bio15)	0.2	1.3
Elevation (m)	0.2	0.7

the top environmental variables associated with codling moth distribution at global level with 64.9, 25.7, and 6.0% average contributions to the model, respectively (Table 3). The jackknife tests of variable importance also showed that these variables had higher predictive

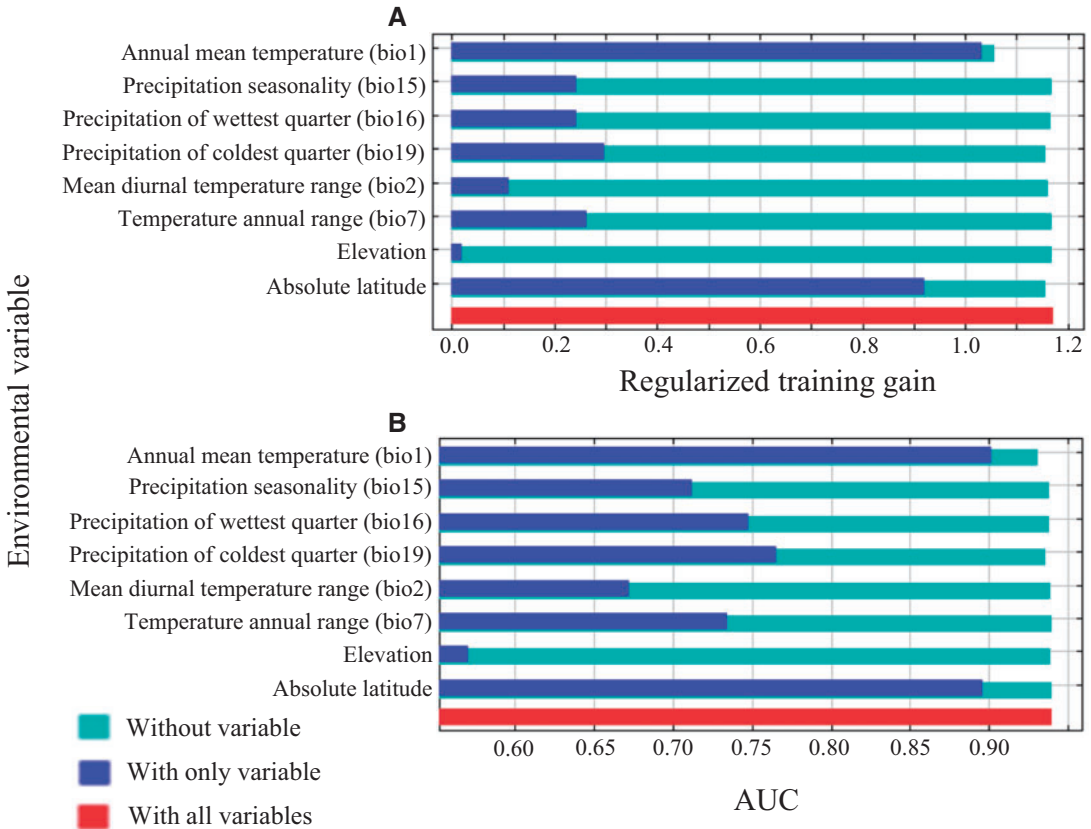


Fig. 3. Relative importance of the environmental variables based on the jackknife test. The figures show each variable's contribution to (A) regularized training gain, and (B) AUC in codling moth model.

power (i.e., high training gain and AUC) than others (Fig. 3). The probability of codling moth presence increased sharply between 0 and 8°C mean annual temperature, was highest at 10°C, and declined sharply after 13°C (Fig. 4A). The probability of presence was higher between 30° and 60° latitudes, and 0 at <20° latitudes and beyond 70° latitudes (Fig. 4B). The probability of codling moth presence was higher in areas of low precipitation during the coldest quarter of the year (Fig. 4C). *Cydia pomonella* had a bi-modal response to mean diurnal range in temperature (Fig. 4D). Latitude had a significant impact on model predictions as the model without latitude predicted codling moth distribution in areas from which codling moth has never been reported (e.g., Ethiopia and Zimbabwe) and it cannot survive because of higher temperature and shorter day length (Supp Fig. 6 [online only]).

CLIMEX model predicted higher growth index for areas where codling moth is currently known to occur (Supp Fig. 7A [online only]). The heat stress index and cold stress index explained why codling moth does not occur in extremely cold northern latitudes and very hot deserts in Africa and parts of Australia (Supp Fig. 7B and C [online only]). The light index from CLIMEX showed areas between 20th parallels not suitable for codling moth (Supp Fig. 7D [online only]).

Discussion

Accurate models for economically important pests' potential distribution are urgently needed for conducting pest risk assessments to facilitate international trade. Our study is the first to present the global potential risk for establishment of codling moth modeled successfully using a correlative niche model MaxEnt and a semi-mechanistic niche model CLIMEX. Our approach can be used for other agricultural pests of quarantine concern. The MaxEnt model used codling moth occurrences and a set of environmental spatial data layers, whereas CLIMEX used published physiological tolerance data for codling moth and in-built climate data layers to predict the potential for establishment. Both models correctly predicted codling moth known occurrences. Models did not predict suitable environmental conditions in countries located between 20°N and 20°S primarily because of shorter photoperiod, and lack of chilling requirement in these areas needed for codling moth to break diapause. Models predicted suitable conditions in a few countries where codling moth currently does not occur but have its preferred host species (i.e., apple). Average annual temperature and latitude (a surrogate for critical photoperiod) were the top environmental variables associated with codling moth distribution.

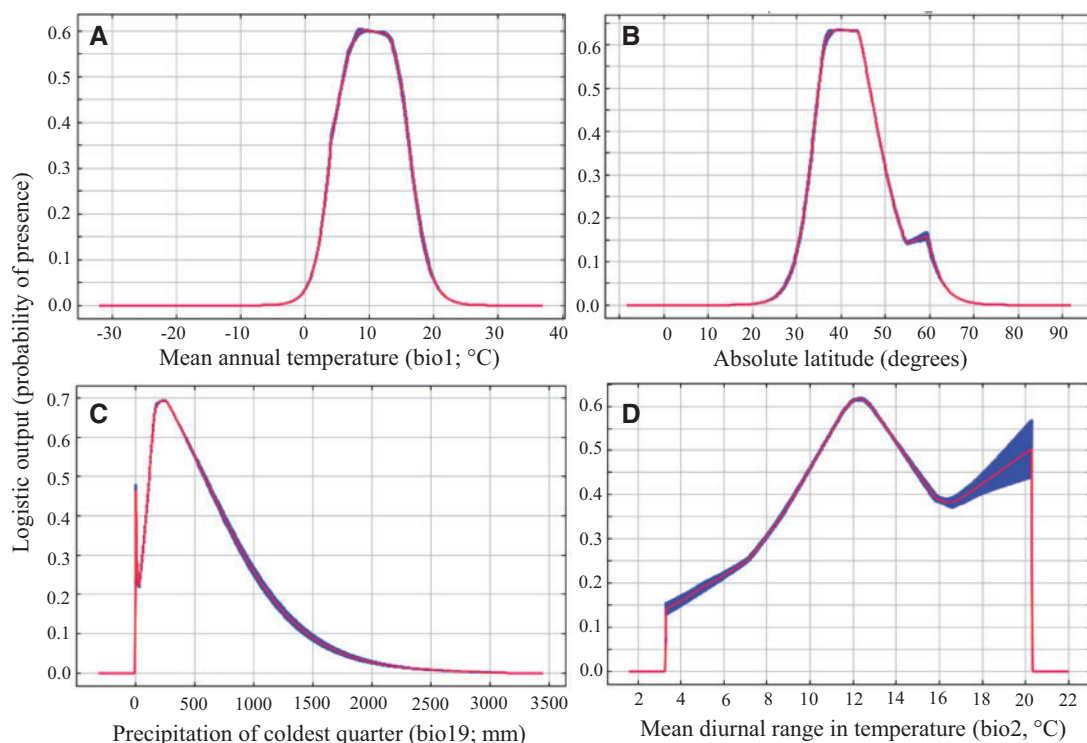


Fig. 4. Response curves of the best predictors of codling moth in the best model; (A) mean annual temperature (bio1; °C), (B) Latitude (degree decimal), (C) precipitation of coldest quarter (bio19; mm), and (D) mean diurnal range in temperature (bio2; °C).

Evaluation of MaxEnt and CLIMEX Models. The best MaxEnt model (Model 1; Table 2) provided a better fit than CLIMEX, which could be because it directly used species presence locations and finer resolution climatic dataset. The performance of MaxEnt was worse at the highest and lowest levels of complexity (Models 9 and 10; Table 2). This suggests that an appropriate level of complexity in correlative niche models is needed to correctly model the species response to environmental factors and to make robust inference. Simpler models often fail to include critical aspects of species–environment relationships (e.g., non-linear responses and variable interactions), whereas complex model over fit the data (Merow et al. 2014). CLIMEX model's poorer performance can be partly attributed to its use of relatively simple functions to model species responses to climatic factors, and coarse resolution climatic dataset. For example, a simpler model by Fowler et al. (2009; a degree-day model using NAPPFAST) overpredicted light brown apple moth [*Epiphyas postvittana* (Walker)] potential distribution, whereas complex models estimated lower risk (Lozier and Mills 2011; MaxEnt model). MaxEnt model, on the other hand, is inherently complex so species-specific tuning was required to achieve optimally complex model (Shcheglovitova and Anderson 2013, Boria et al. 2014). Elevation was identified as an important factor associated with codling moth distribution because a model with elevation as a predictor

performed better than the model without it (Models 1 and 7; Table 2). This matches with Jones et al. (2013) study that showed a strong influence of latitude and elevation in predicting codling moth spring emergence in North America.

Global Projections of Codling Moth Distribution. Predictions from both models matched closely with the currently known global distribution of codling moth and its preferred host plant, apples (Figs. 1 and 2). For example, both models predicted codling moth distribution in southern Norway, Sweden, and Finland which matched with the reports of its occurrence in these countries (Saethre and Edland 2001, Rafoss and Saethre 2003). Our models predicted more potentially suitable areas for codling moth in China than models published by Yang (2008) and Liang (2010), which may be because our models included higher number of occurrences covering more regions of China. It could also be because of the fact that their models used data from only China (i.e., invaded range) and we used global data (native and invaded range); the regional model may have underestimated codling moth potential suitable areas because it did not include all the environment conditions where this species occurs (Broennimann et al. 2007, Fitzpatrick et al. 2007, Sanchez-Fernandez et al. 2011). This may also be the case for Rafoss and Saethre (2003) model predictions in Norway. MaxEnt model predicted codling moth distribution in southern Alaska, which matched

with reports from the [Discover Life \(2014\)](#) and University of Alaska, Fairbanks Cooperative Extension Service ([UAF 2014](#)). Disagreements between CLIMEX and MaxEnt model spatial predictions may be because of their use of different types and spatial resolutions of climatic datasets, levels of complexity in model fitting, and their specific assumptions ([Elith et al. 2011](#), [Sutherst et al. 2007](#)).

Latitude, a surrogate for the number of daylight hours, had a profound impact on codling moth potential distribution ([Supp Fig. 6B \[online only\]](#)). A MaxEnt model without latitude as a variable predicted marginally suitable areas for codling moth in countries such as Bolivia, Ecuador, Peru, and western Ethiopia from where codling moth has never been reported, and its diapause requirement in those areas will not be met; codling moth requires a critical photoperiod ([Neven 2012, 2013](#)), which is not met in these countries. Therefore, this model was discarded and a model with latitude was selected ([Supp Fig. 6A \[online only\]](#)). CLIMEX model showed that light index in these regions was 0; indicating no growth ([Supp Fig. 7D \[online only\]](#)).

Caveats and Uncertainties. Results from this study should be interpreted cautiously given some of the inherent uncertainties associated with niche models. For example, niche model predictions may be affected by the quality of occurrence data, sampling bias, resolution of spatial data layers, species characteristics, and spatial autocorrelation ([Guisan et al. 2007a,b](#); [Taylor and Kumar 2012](#); [Anderson 2013](#); [Dormann et al. 2013](#); [Syfert et al. 2013](#)). The physiological temperature and moisture thresholds generated in laboratory studies for codling moth may not have covered the entire range of genetic and phenotypic variability in codling moth populations globally; CLIMEX parameters have uncertainties ([Taylor and Kumar 2012](#)). MaxEnt model is also affected by different decisions made during model calibration; for example, selection of background points and extent, value of RM, and selection of feature types can have immense influences on model predictions ([Barve et al. 2011](#), [Owens et al. 2013](#), [Shcheglovitova and Anderson 2013](#), [Boria et al. 2014](#)). Our validation of MaxEnt predictions using a semi-mechanistic CLIMEX model shows that decisions made during calibration for codling moth MaxEnt model were appropriate because the model projections broadly matched observations in major parts of the world ([Figs. 1 and 2](#); [Supp Figs. 1–5 \[online only\]](#)).

Future climate change may alter codling moth distribution; for example, with increasing global temperatures, areas that currently have marginal suitability (average annual temperature $\sim 9^{\circ}\text{C}$) for codling moth would become more suitable and areas with higher average annual temperature ($>34^{\circ}\text{C}$) would become unsuitable. Further studies are needed to investigate the effects of potential climate change on codling moth distribution and biology because changes in temperature and moisture might alter insect pests' population growth rates, increase the number of generations, extend the development season, and modify the crop-pest synchrony and interspecific interactions ([Porter](#)

[et al. 1991](#)). A better temporal resolution climate data may be needed for insect pest establishment predictive models because monthly averaged climatic data such as available from WorldClim ([Hijmans et al. 2005](#)) may not be appropriate for some insect pests that have critical physiological requirements of weekly or daily minimum temperature ([Kumar et al. 2014a](#)). In addition to suitable climate, the likelihood of establishment of an insect pest in new geographic areas is also affected by the propagule pressure (i.e., the number of individuals of a species introduced to a novel region), presence of host plant species, and other abiotic factors and biotic interactions (e.g., presence of competitors and natural enemies) ([Thuiller et al. 2005](#), [Saikkonen et al. 2012](#), [Bacon et al. 2014](#)). Our models predicted climatic suitability in several areas, where codling moth currently does not occur (e.g., South Korea and Japan) which may be because of very low propagule pressure, dispersal barriers, and presence of natural enemies in these regions. The propagule pressure in different parts of the world depends on the frequency and amount of fruit imports and the likelihood of these fruits being infested with codling moth.

International Trade Implications for Biosecurity. Our results can be used to help guide pest risk assessments by the national plant protection organizations, monitoring for unintentional introductions of codling moth in different countries, and policy makers and trade negotiators in making science-based decisions. In addition, in countries like China, which is dealing with a relatively recent introduction and spread of codling moth ([Yang 2008](#), [Liang 2010](#), [Zhang et al. 2012](#)), these maps can be used to *identify areas most at risk* of the expansion of this pest. Efforts can be coordinated and concentrated strategically across susceptible areas to stem the incursion. Countries like Japan and South Korea where codling moth currently does not occur can use these results for effective monitoring and surveillance of potential introduction of this pest via trade from currently infested countries and/or all countries with high climatic suitability. An additional potential application of these maps is the identification of areas most suitable for area-wide pest suppression, sterile insect technique, or eradication. Areas with established populations of codling moth which are on the extreme margins of climate suitability can be targeted as the most likely locations for these suppression and eradication efforts.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

Acknowledgments

This research was funded by a grant through the Washington Tree Fruit Research Commission (WTFRC) from the Foreign Agricultural Service of the U.S. Department of Agriculture (USDA). We thank Mike Willett (Northwest Horticultural Council [NHC]), James McFerson and Kathy Coffey (WTFRC), and Michele Watkins (U.S. Department of

Agriculture Agricultural Research Service [USDA-ARS]) for providing occurrence data and assistance during the project. We thank Paul Ode (Colorado State University), Daniel Manier (U.S. Geological Survey), and Hossein A.N. Khandan (University of Florida) for their comments on earlier versions of the manuscript. We also thank the Natural Resource Ecology Laboratory at Colorado State University, and Yakima Agricultural Research Laboratory, USDA-ARS, Wapato, WA, for providing the logistical support. Finally, we are grateful to two anonymous reviewers whose comments also improved the manuscript.

References Cited

- Anderson, R. P. 2013.** A framework for using niche models to estimate impacts of climate change on species distributions, pp. 8–28. *In* A. L. Angert, S. L. LaDeau, and R. S. Ostfeld (eds.), *Climate change and species interactions: Ways Forward*. Annals of the New York Academy of Sciences, New York, NY.
- Anonymous. 2014a.** Bionomics of codling moth: Introduction. (<http://ipmnet.org/codlingmoth/bionomics/about.html>) (accessed 18 June 2015).
- Anonymous. 2014b.** Bionomics of codling moth: Effects of rainfall and humidity. (<http://ipmnet.org/codlingmoth/bionomics/humidity.html>) (accessed 18 June 2015).
- Anonymous. 2014c.** Bionomics of codling moth: Effect of photoperiod on codling moth. (<http://ipmnet.org/codlingmoth/bionomics/photoperiod.html>) (accessed 18 June 2015).
- Anonymous. 2014d.** Bionomics of codling moth: Diapause induction in codling moth larvae. (<http://ipmnet.org/codlingmoth/bionomics/diapause.html>) (accessed 18 June 2015).
- Bacon, S. J., A. Aebi, P. Calanca, and S. Bacher. 2014.** Quarantine arthropod invasions in Europe: The role of climate, hosts and propagule pressure. *Divers. Distrib.* 20: 84–94.
- Barve, N. 2008.** Tool for Partial-ROC ver 1.0; Biodiversity Institute, Lawrence, Kansas. (<http://biodiversity-informatics-training.org/software-data-sources/>) (accessed 18 June 2015).
- Barve, N., V. Barve, A. Jimenez-Valverde, A. Lira-Noriega, S. P. Maher, A. T. Peterson, J. Soberon, and F. Villalobos. 2011.** The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecol. Model.* 222: 1810–1819.
- Barnes, M. M. 1991.** Tortricids in pome and stone fruits. 5.1.1 Codling moth occurrence, host race formation and damage, pp. 313–327. *In* L.P.S. van der Geest and H. H. Evenhuis (eds.), *Tortricid pests: Their biology, natural enemies and control*, Chapter 5. Elsevier, Amsterdam, The Netherlands.
- Beers, E. H., J. F. Brunner, M. J. Willett, and G. M. Warner. 1993.** Orchard pest management: A resource book for the Pacific Northwest. Good Fruit Grower, Yakima, WA.
- Beers, E. H., D. M. Suckling, R. J. Prokopy, and J. Avilla. 2003.** Ecology and management of apple arthropod pests, pp. 489–519. *In* D. C. Ferree and I. J. Warrington (eds.), *Apples: Botany, production and uses*. CAB International, Wallington, Oxford, United Kingdom.
- Blomefield, T. L., and J. H. Giliomee. 2011.** Effect of temperature on the oviposition, longevity and mating of codling moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae). *Afr. Entomol.* 19: 42–60.
- Boria, R. A., L. E. Olson, S. M. Goodman, and R. P. Anderson. 2014.** Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol. Model.* 275: 73–77.
- Broennimann, O., U. A. Treier, H. Muller-Scharer, W. Thuiller, A. T. Peterson, and A. Guisan. 2007.** Evidence of climatic niche shift during biological invasion. *Ecol. Lett.* 10: 701–709.
- Brown, J. L. 2014.** SDMtoolbox: A python-based GIS toolkit for landscape genetic, biogeographic and species distribution model analyses. *Methods Ecol. Evol.* 5: 694–700.
- Dadvand, P., X. Basagana, J. Barrera-Gomez, B. Diffey, and M. Nieuwenhuijsen. 2011.** Measurement errors in the assessment of exposure to solar ultraviolet radiation and its impact on risk estimates in epidemiological studies. *Photochem. Photobiol. Sci.* 10: 1161–1168.
- De Meyer, M., M. P. Robertson, M. W. Mansell, S. Ekesi, K. Tsuruta, W. Mwaiko, J. F. Vayssières, and A. T. Peterson. 2010.** Ecological niche and potential geographic distribution of the invasive fruit fly *Bactrocera invadens* (Diptera, Tephritidae). *Bull. Entomol. Res.* 100: 35–48.
- Discover Life 2014.** Discover Life. (<http://www.discoverlife.org/mp/20l?id=GBIF773809983>) (accessed 18 June 2015).
- Dormann, C. F., S. J. Schymanski, J. Cabral, I. Chuine, C. Graham, F. Hartig, M. Kearney, X. Morin, C. Romermann, B. Schroder, et al. 2012.** Correlation and process in species distribution models: bridging a dichotomy. *J. Biogeogr.* 39: 2119–2131.
- Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carre, J.R.G. Marquez, B. Gruber, B. Lafourcade, P. J. Leita, et al. 2013.** Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 27–46.
- Elith, J. 2015.** Chapter 6: Predicting distributions of invasive species. (<http://arxiv.org/ftp/arxiv/papers/1312/1312.0851.pdf>) (accessed 18 June 2015).
- Elith, J., S. J. Phillips, T. Hastie, M. Dudik, Y. E. Chee, and C. J. Yates. 2011.** A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* 17: 43–57.
- Enquist, B. J., and K. J. Niklas. 2001.** Invariant scaling relations across tree-dominated communities. *Nature* 410: 655–660.
- (ESRI) Environmental Systems Research Institute. 2013.** ArcGIS 10.2 desktop. Environmental Systems Research Institute (ESRI), Redlands, CA.
- Evangelista, P. H., S. Kumar, T. J. Stohlgren, and N. E. Young. 2011.** Assessing forest vulnerability and the potential distribution of pine beetles under current and future climate scenarios in the Interior West of the US. *For. Ecol. Manag.* 262: 307–316.
- Fitzpatrick, M. C., J. F. Weltzin, N. J. Sanders, and R. R. Dunn. 2007.** The biogeography of prediction error: Why does the introduced range of the fire ant over-predict its native range? *Glob. Ecol. Biogeogr.* 16: 24–33.
- Fowler, G., L. Garrett, A. Neeley, R. Magarey, D. Borchert, and B. Spears. 2009.** Economic analysis: Risk to U.S. apple, grape, orange and pear production from the light brown apple moth, *Epiphyas postvittana* (Walker). U.S. Department of Agriculture-Animal and Plant Health Inspection Service.
- Franklin, J. 2009.** Mapping species distributions: Spatial inference and prediction. Cambridge University Press, Cambridge, United Kingdom.
- Guisan, A., C. H. Graham, J. Elith, F. Huettmann, and NCEAS Species Distribution Modeling Group. 2007a.** Sensitivity of predictive species distribution models to change in grain size. *Divers. Distrib.* 13: 332–340.
- Guisan, A., N. E. Zimmermann, J. Elith, C. H. Graham, S. Phillips, and A. T. Peterson. 2007b.** What matters for predicting the occurrences of trees: Techniques, data, or species' characteristics? *Ecol. Monogr.* 77: 615–630.
- Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005.** Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* 25: 1965–1978.

- Howell, J. F., and L. G. Neven. 2000. Physiological development time and zero development temperature of the codling moth (Lepidoptera: Tortricidae). *Environ. Entomol.* 29: 766–772.
- Ireland, K. B., G. E. S. Hardy, and D. J. Kriticos. 2013. Combining inferential and deductive approaches to estimate the potential geographical range of the invasive plant pathogen, *Phytophthora ramorum*. *PLoS ONE* 8.
- Jetz, W., C. H. Sekercioglu, and K. Bohning-Gaese. 2008. The worldwide variation in avian clutch size across species and space. *PLoS Biol.* 6: 2650–2657.
- Jones, V. P., R. Hilton, J. F. Brunner, W. J. Bentley, D. G. Alston, B. Barrett, R. A. Van Steenwyk, L. A. Hull, J. F. Walgenbach, W. W. Coates, et al. 2013. Predicting the emergence of the codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae), on a degree-day scale in North America. *Pest Manag. Sci.* 69: 1393–1398.
- Kiritani, K. 2006. Predicting impacts of global warming on population dynamics and distribution of arthropods in Japan. *Popul. Ecol.* 48: 5–12.
- Knight, A. L. 2008. Codling moth areawide integrated pest management, pp. 159–190. In O. Koul, G. W. Cuperus and N. Elliott (eds.), *Area-wide pest management: Theory and Implementation*. CAB International, United Kingdom.
- Kriticos, D. J., R. W. Sutherst, J. R. Brown, S. W. Adkins, and G. F. Maywald. 2003. Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp *indica* in Australia. *J. Appl. Ecol.* 40: 111–124.
- Kriticos, D. J., P. Reynaud, R. H. A. Baker, and D. Eyre. 2012a. Estimating the global area of potential establishment for the western corn rootworm (*Diabrotica virgifera virgifera*) under rain-fed and irrigated agriculture. *EPPO Bull.* 42: 56–64.
- Kriticos, D. J., B. L. Webber, A. Leriche, N. Ota, I. Macadam, J. Bathols, and J. K. Scott. 2012. CliMond: global high-resolution historical and future scenario climate surfaces for bioclimatic modelling. *Methods Ecol. Evol.* 3: 53–64.
- Kumar, S., L. G. Neven, and W. L. Yee. 2014a. Assessing the potential for establishment of western cherry fruit fly using ecological niche modeling. *J. Econ. Entomol.* 107: 1032–1044.
- Kumar, S., L. G. Neven, and W. L. Yee. 2014b. Evaluating correlative and mechanistic niche models for assessing the risk of pest establishment. *Ecosphere* 5: 1–23.
- Kumar, S., J. Graham, A. M. West, and P. H. Evangelista. 2014c. Using district-level occurrences in MaxEnt for predicting the invasion potential of an exotic insect pest in India. *Comp. Elect. Agric.* 103: 55–62.
- Li, B. N., J. Ma, X. N. Hu, H. J. Liu, and R. J. Zhang. 2009. Potential geographical distributions of the fruit flies *Ceratitis capitata*, *Ceratitis cosyra*, and *Ceratitis rosa* in China. *J. Econ. Entomol.* 102: 1781–1790.
- Liang, L., Y. Hui, L. Xingyue, Z. Junhua, C. Zaizhing, and Y. Ding. 2010. Analysis of suitability of the codling moth, *Cydia pomonella* in China. *Plant Prot.* 36: 101–105.
- Lloyd, D. C. 1960. Memorandum on natural enemies of the codling moth, *Cydia pomonella* (L.). Commonw. Inst. Biol. Control Mimeo, 40.
- Lozier, J. D., and N. J. Mills. 2011. Predicting the potential invasive range of light brown apple moth (*Epiphyas postvittana*) using biologically informed and correlative species distribution models. *Biol. Invasions* 13: 2409–2421.
- Mani, E., and T. Wildbolz. 1977. The dispersal of male codling moths (*Laspeyresia pomonella* L.) in the Upper Rhine Valley. *J. Appl. Entomol.* 83: 161–168.
- Merow, C., M. J. Smith, T. C. Edwards, A. Guisan, S. M. McMahon, S. Normand, W. Thuiller, R. O. Wüest, N. E. Zimmermann, and J. Elith. 2014. What do we gain from simplicity versus complexity in species distribution models? *Ecography* 37: 1267–1281.
- Neven, L. G. 2012. Fate of codling moth (Lepidoptera: Tortricidae) in harvested apples held under short photoperiod. *J. Econ. Entomol.* 105: 297–303.
- Neven, L. G. 2013. Effects of short photoperiod on codling moth diapause and survival. *J. Econ. Entomol.* 106: 520–523.
- Neven, L. G., H. J. Ferguson, and A. Knight. 2000. Sub-zero cooling synchronizes post-diapause development of codling moth, *Cydia pomonella*. *Cryo-Letters* 21: 203–214.
- Owens, H. L., L. P. Campbell, L. L. Dornak, E. E. Saupe, N. Barve, J. Soberon, K. Ingenloff, A. Lira-Noriega, C. M. Hensz, C. E. Myers, et al. 2013. Constraints on interpretation of ecological niche models by limited environmental ranges on calibration areas. *Ecol. Model.* 263: 10–18.
- Peterson, A. T., J. Soberon, R. G. Pearson, R. P. Anderson, E. Martinez-Meyer, M. Nakamura, and M. B. Araujo. 2011. *Ecological niches and geographic distributions*. Princeton University Press, Princeton, NJ.
- Phillips, S. J. 2008. Transferability, sample selection bias and background data in presence-only modelling: A response to Peterson et al. (2007). *Ecography* 31: 272–278.
- Phillips, S. J., and M. Dudik. 2008. Modeling of species distributions with Maxent: New extensions and a comprehensive evaluation. *Ecography* 31: 161–175.
- Phillips, S. J., R. P. Anderson, and R. E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.* 190: 231–259.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50: 53–65.
- Pitcairn, M. J., C. Pickel, L. A. Falcon, and F. G. Zalom. 1991. Development and survivorship of *Cydia pomonella* (L.) (Lepidoptera: Tortricidae) at ten constant temperatures. *Pan-Pac. Entomol.* 67: 189–194.
- Porter, J. H., M. L. Parry, and T. R. Carter. 1991. The potential effects of climate-change on agricultural insect pests. *Agric. For. Meteorol.* 57: 221–240.
- Proverbs, M. D., and J. R. Newton. 1962. Effect of heat on the fertility of the codling moth, *Carpocapsa pomonella* (L.) (Lepidoptera: Olethreutidae). *Can. Entomol.* 94: 225–233.
- Rafoss, T., and M. G. Saethre. 2003. Spatial and temporal distribution of bioclimatic potential for the Codling moth and the Colorado potato beetle in Norway: Model predictions versus climate and field data from the 1990s. *Agric. For. Entomol.* 5: 75–85.
- Riedl, H. 1983. Analysis of codling moth phenology in relation to latitude, climate and food availability, pp. 233–252. In: V. K. Brown and I. Hodek (eds.), *Diapause and life cycle strategies in insects*. Dr. W. Junk, The Hague, The Netherlands.
- Riedl, H., and B. A. Croft. 1978. The effects of photoperiod and effective temperatures on the seasonal phenology of the codling moth (Lepidoptera: Tortricidae). *Can. Entomol.* 110: 455–470.
- Rock, G. C., and P. L. Shaffer. 1983. Developmental rates of codling moth (Lepidoptera: Olethreutidae) reared on apple at four constant temperatures. *Environ. Entomol.* 12: 831–834.
- Saethre, M. G., and T. Hofsvang. 2002. Effect of temperature on oviposition behavior, fecundity, and fertility in two northern European populations of the codling moth (Lepidoptera: Tortricidae). *Environ. Entomol.* 31: 804–815.
- Saethre, M.-G., and T. Edland. 2001. Distribution of the codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae) in southern Norway. *Nor. J. Entomol.* 48: 251–262.
- Saikkonen, K., K. Taulavuori, T. Hyvonen, P. E. Gundel, C. E. Hamilton, I. Vanninen, A. Nissinen, and M.

- Helander, 2012.** Climate change-driven species' range shifts filtered by photoperiodism. *Nat. Clim. Change* 2: 239–242.
- Sambaraju, K. R., A. L. Carroll, J. Zhu, K. Stahl, R. D. Moore, and B. H. Aukema. 2012.** Climate change could alter the distribution of mountain pine beetle outbreaks in western Canada. *Ecography* 35: 211–223.
- Sanchez-Fernandez, D., J. M. Lobo, and O. L. Hernandez-Manrique. 2011.** Species distribution models that do not incorporate global data misrepresent potential distributions: a case study using Iberian diving beetles. *Diver. Distrib.* 17: 163–171.
- Shcheglovitova, M., and R. P. Anderson. 2013.** Estimating optimal complexity for ecological niche models: A jackknife approach for species with small sample sizes. *Ecol. Model.* 269: 9–17.
- Shel'deshova, G. G. 1967.** Ecological factors determining distribution of the codling moth, *Laspeyresia pomonella* L. (Lepidoptera: Tortricidae), in northern and southern hemispheres. *Entomol. Rev.* 46: 349–361.
- Slingerland, M. V. 1898.** Codling moth in New England in 1750. *New York Agr. Expt. Sta. Bull.* (Cornell), 142: 85–155.
- Soberon, J., and A. T. Peterson. 2005.** Interpretation of models of fundamental ecological niches and species' distributional areas. *Biodivers. Informatics* 2: 1–10.
- Stoeckli, S., M. Hirschi, C. Spirig, P. Calanca, M. W. Rotach, and J. Samietz. 2012.** Impact of climate change on voltinism and prospective diapause induction of a global pest insect - *Cydia pomonella* (L.). *PLoS ONE* 7.
- Sutherst, R. W., and G. F. Maywald. 1985.** A computerized system for matching climates in ecology. *Agric. Ecosyst. Environ.* 13: 281–299.
- Sutherst, R. W., G. F. Maywald, and D. J. Kriticos. 2007.** CLIMEX Version 3: User's Guide: Hearne Scientific Software Pty Ltd, (<http://www.hearne.com.au/attachments/CLIMEXUserGuide3.pdf>) (accessed 18 June 2015).
- Syfert, M. M., M. J. Smith, and D. A. Coomes. 2013.** The effects of sampling bias and model complexity on the predictive performance of MaxEnt species distribution models. *PLoS ONE* 8: e55158.
- Taylor, S., and L. Kumar. 2012.** Sensitivity analysis of CLIMEX parameters in modelling potential distribution of *Lantana camara* L. *PLoS ONE* 7.
- Thuiller, W., D. M. Richardson, P. Pysek, G. F. Midgley, G. O. Hughes, and M. Rouget. 2005.** Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. *Glob. Change Biol.* 11: 2234–2250.
- Tuda, M., T. Matsumoto, T. Itioka, N. Ishida, M. Takanashi, W. Ashihara, M. Kohyama, and M. Takagi. 2006.** Climatic and intertrophic effects detected in 10-year population dynamics of biological control of the arrowhead scale by two parasitoids in southwestern Japan. *Popul. Ecol.* 48: 59–70.
- UAF 2014.** University of Alaska fairbanks cooperative extension service; Chapter 12: Home Orchards, (<http://www.uaf.edu/files/ces/districts/tanana/mg/manual/12-Home-Orchards.pdf>) (accessed 18 June 2015).
- Veloz, S. D. 2009.** Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *J. Biogeogr.* 36: 2290–2299.
- Warren, D. L., R. E. Glor, and M. Turelli. 2010.** ENMTools: A toolbox for comparative studies of environmental niche models. *Ecography* 33: 607–611.
- Webber, B. L., C. J. Yates, D. C. Le Maitre, J. K. Scott, D. J. Kriticos, N. Ota, A. McNeill, J. J. Le Roux, and G. F. Midgley. 2011.** Modelling horses for novel climate courses: Insights from projecting potential distributions of native and alien Australian acacias with correlative and mechanistic models. *Divers. Distrib.* 17: 978–1000.
- Willett, M. J., L. Neven, and C. E. Miller. 2009.** The occurrence of codling moth in low latitude countries: Validation of pest distribution reports. *Horttechnology* 19: 633–637.
- Weitzner, P., and M. E. Whalon. 1987.** Head capsule widths as an indicator of the larval instar of codling moth (Lepidoptera: Olethreutidae). *Great Lakes Entomol.* 20: 147–150.
- World Trade Organization. 2014.** The WTO agreement on the application of sanitary and phytosanitary measures (SPS Agreement). (http://www.wto.org/english/tratop_e/sps_e/spsagr_e.htm) (accessed 18 June 2015).
- Yang, R. 2008.** Study on habitat suitability of *Cydia pomonella* (L.) in China, pp. 76. Northwest University of Science and Technology, Yangling, Shaanxi, China.
- Zhang, R. Z., F. X. Wang, Y. L. Zhang, H. J. Chen, J. C. Luo, Q. Y. Wang, W. X. Liu, M. Ainiwaer, C. J. Pu, Y. G. Yan, et al. 2012.** Progress on monitoring and control of the codling moth, *Cydia pomonella* (L.). *Chin. J. Appl. Entomol.* 49: 37–42.

Received 22 December 2014; accepted 5 June 2015.