

THE IMPORTANCE OF *OPUNTIA* IN MEXICO AND ROUTES OF INVASION AND IMPACT OF *CACTOBLASTIS CACTORUM* (LEPIDOPTERA: PYRALIDAE)

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ABSTRACT

The appearance of the cactus moth *Cactoblastis cactorum* in Florida has roused concern over its possible effects on the *Opuntia*-rich areas of Mexico and the southwestern United States. In this paper we discuss the economic importance of *Opuntia* in Mexico and propose a method to predict the invasion of the alien species *C. cactorum*. In Mexico, the products derived from *Opuntia* are mainly human food and fodder for livestock. Both cultivated and wild populations of *Opuntia* are currently used for these two purposes. By using bioclimatic modeling, we predicted the potential distribution of *C. cactorum* and overlaid this on the actual distribution of *Opuntia* species. The resulting maps indicate that the possible routes of invasion to Mexico are 1) along the northern border through Texas (most likely) and 2) via southeastern Mexico (less likely). The impacts of an invasion of *C. cactorum* on *Opuntia* products could be significant as well as being a threat to endemic species. Bioclimatic modeling can help to predict the areas of highest probability of attack and facilitate planning to mitigate future impacts.

Key Words: bioclimatic modeling, GARP, FloraMap, cactus

RESUMEN

El uso de agentes de control biológico y sus efectos sobre especies nativas ha generado polémica. La invasión de la palomilla del nopal al continente norteamericano ha provocado preocupación acerca de la posible introducción de esta especie exótica a zonas de alta riqueza de *Opuntias* endémicas de México. En este trabajo hacemos énfasis en la importancia económica de los productos de *Opuntia* en México y proponemos un método que predice la invasión de *C. cactorum*. Usamos modelos bioclimáticos para generar las distribuciones potenciales de *C. cactorum* y especies de *Opuntia*. Los mapas resultantes permiten predecir la ruta de invasión de la palomilla del nopal al territorio Mexicano. Los mapas de probabilidad generados por FloraMap sugieren dos posibles rutas de invasión, la primera con alta probabilidad vía la frontera norte del país en Texas y una ruta secundaria por el Sureste mexicano. El impacto de *C. cactorum* y el potencial de los modelos bioclimáticos son discutidos.

The textbook example of successful biological control, the moth *Cactoblastis cactorum* (Berg) on *Opuntia* species in Australia, has now become a problem of major concern for continental North America (e.g., Zimmerman et al. 2000). The consequences of the arrival of *C. cactorum* on the *Opuntia* rich regions of the southwestern U.S. and Mexico, as well as the possible economic and social impact on Mexican urban and rural human populations has only recently been addressed (Zimmerman et al. 2000). The purpose of this paper is twofold. On one hand, it addresses the importance of *Opuntia* products in Mexico from an economic and social status, and on the other it proposes a means of modeling the routes of invasion and assessing the areas of Mexico that could be most susceptible to a possible invasion of *C. cactorum*.

THE IMPORTANCE OF *OPUNTIA* IN MEXICO

In present-day Mexico, there is a large array of traditional and commercial uses of *Opuntia* (Platyopuntia: Cactaceae). Historically the hunter-gatherer communities that roamed the southwestern U.S. and Mexico were using products derived from *Opuntia* (mainly forage, fruit and vegetables) in 9,000 BC. The process of domestication of a few species of *Opuntia* may have started as far in the past as 6000 BC (Smith 1967). By 3000 BC, hunter-gatherers settled into small communities, where family owned plots contained species of *Opuntia* that had been collected from wild populations (Hoffmann 1995). During the 1850s *Opuntia* was commonly used in the growing cattle ranching industry of the Sonoran and Chihuahuan deserts which gave way to

an extensive use of *Opuntia* as fodder. Due to the increase in population over the past 50 years, the demand for *Opuntia* products has increased dramatically. As family owned plots were not enough to satisfy demand, plantations were developed surrounding the most important urban areas. There are three main consequences of the use of products derived from the Cactaceae on a large scale: 1) an increase in hybridization between species that were brought in from wild populations to family owned plots, 2) a continuous use of wild populations for forage as well as for vegetables, and 3) a decrease in morphological diversity within plots (Casas et al. 1999) which could eventually lead to a decrease in genetic variation (Colunga-Garcia et al. 1999). However, despite the important commercial aspect of cactus products, the wild populations found around family-owned plots are still used for subsistence in the dry regions of Mexico and represent the transition between the wild and cultivated species, thus making them important gene pools of domesticated varieties.

The genus *Opuntia* is one of the most used plants in Mexico and Central America. Due to the high protein and fiber contents found in cladodes, and the amount of water in tissues (88-91%, Pimienta 1990), the range of uses given to *Opuntia* has been extremely wide, from food to cosmetics and adhesives (Barbera 1995). In Mexico, traditional uses of *Opuntia* vary widely although there are two main products that account for the economical importance of *Opuntia* products: food and fodder (Pimienta 1990; Barbera 1995). Fodder is mainly for cattle and goats in all parts of Mexico. The use of cactus for forage has also been documented in many other parts of the world including the U.S., northern and southern Africa, and several South American countries (Felker 1995). For example, in Brazil close to 300,000 ha are used to produce fodder (Barbera 1995). As food, *Opuntia* can be consumed as vegetables (by dicing young cladodes) or as fruit (cactus pears). Production of fruits is found in 15 out of 32 Mexican states employing close to 20,000 people, whereas use as vegetables is found in 14 states and employs close to 8,000 people. In addition, most rural people use prickly pear products from local wild populations or maintain family-owned plots for self-consumption.

In Mexico there are >250,000 ha of *Opuntia* cultivated for all purposes (Flores-Valdez & Aguirre-Rivera 1979; SAGAR 1995-1998). The area that is used for cultivation of fodder is close to 150,000 ha out of which 500 ha are being used intensively in the state of Jalisco. Most of the area under cultivation is used as forage for cattle farming. These areas are a remnant of areas that were designed to improve carrying capacity of impoverished rural areas during the 1970s and 1980s and were designed to introduce extensive cattle

ranching and prickly pear production (Barbera 1995). After the failure of such programs, most of the areas that were cultivated were left behind and are still being used today as forage (Pimienta 1990). Wild *Opuntia* populations are used extensively for fodder and at least 12 species are known to be used as forage (Table 1); this figure is probably conservative as most local wild populations are also commonly being used.

Mexico has the highest variety of cultivated species of prickly pear (8 species and over 11 varieties, Flores-Valdez & Gallegos 1993) and is an important area in Cactaceae biodiversity.

Economically, *Opuntia* products constitute close to 1.5% of total agricultural production and represent 2.5% of the value of agricultural products (SAGAR 1995-1998, Fig. 1). The production of both cactus pears and cladodes used as vegetables have increased over the past eight years (Fig. 2). This increase has occurred primarily because of better management practices (Pimienta 1990); total area under production has not increased to the same degree. The average income generated by *Opuntia* products over the period 1990-1998 is approximately \$50 million U.S. per year, with vegetable usage constituting more than half of the value (\$27 million), followed by cactus pears (\$20 million), and finally fodder (\$1 million). In addition, the export market of *Opuntia* products is valued at \$50 million per year. Exports are mainly to the U.S., Canada, Europe, and Japan.

In addition to their value to humans, opuntias are common and often dominant components of natural floras, where they have substantial environmental importance. Species of the Cactaceae and specifically those of *Opuntia* are a major ecological component of the floras of the Chihuahuan and Sonoran Deserts (nopaleras). They are a major contributor to soil stability. They constitute an important dietary component of white tailed and mule deer (*Odocoileus virginianus* Zimmermann and *O. hemionus* (Rafinesque)), rodents (*Peromyscus* spp., *Neotoma albigula* Hartley and *Dipodomys* spp.), javelinas (*Pecari tajacu* L.), and coyotes (*Canis latrans* Say) (Mandujano et al. 1997; Montiel & Montaña 2000). They also provide nesting sites and food for a variety of insects, birds, rodents, and lagomorphs (Gonzalez-Espinosa & Quintana-Asensio 1986; Russell & Felker 1987).

Mexico has one of the highest species diversity of *Opuntia* and populations cover an area of close to 3,000,000 ha (1.5% of Mexican territory). The numbers of *Opuntia* species varies in the literature, partially because of frequent hybridization between species and the lack of a standardized classification scheme. Bravo-Hollis (1978) recognized 104 species of *Opuntia* in Mexico, 56 of which are in the subgenus *Platyopuntia*, (prickly-pears), 38 of which are endemic.

Although some authors have suggested that *C. cactorum* may already be present in southeast-

TABLE 1. SPECIES OF *OPUNTIA* EVALUATED IN DISTRIBUTION STUDY, THOSE USED AS FORAGE OR FOR FRUIT OR VEGETABLES, AND THOSE KNOWN TO BE ATTACKED BY *CACTOBLASTIS CACTORUM*. TAXONOMIC STATUS WAS DETERMINED USING BRAVO-HOLLIS 1978 AND BRAVO-HOLLIS AND SANCHEZ-MEJORADA 1991.

<i>Opuntia</i> sp.	Used as forage	Used as fruit and/or vegetables	Known to be affected by <i>C. cactorum</i>
<i>amyclaea</i>		X	
<i>atrispina</i>			
<i>atropes</i>			
<i>azurea</i>	X		
<i>bensonii</i>			
<i>bravoana</i>			
<i>cantabrigiensis</i>	X		
<i>chavena</i>			
<i>chlorotica</i>			
<i>decumbens</i>			
<i>depressa</i>			
<i>dillenii</i>			
<i>durangensis</i>	X		
<i>engelmannii</i>	X		
<i>excelsa</i>			
<i>figus-indica</i>		X	X
<i>fulginosa</i>			
<i>hucajuapensis</i>			
<i>hyptiacantha</i>		X	
<i>jaliscana</i>			
<i>joconostle</i>			
<i>lagunae</i>			
<i>lasiacantha</i>			
<i>leucotricha</i>	X	X	
<i>lindheimeri</i>	X		X
<i>littoralis</i>			
<i>macrorrhiza</i>			
<i>megacantha</i>		X	X
<i>megarhiza</i>			
<i>microdasys</i>			
<i>oricola</i>			
<i>pachona</i>			
<i>phaeacantha</i>	X		
<i>pilifera</i>			
<i>puberula</i>			
<i>pubescens</i>			
<i>pumila</i>			
<i>pycnantha</i>			
<i>rastrera</i>	X		
<i>rileyi</i>			
<i>robusta</i>	X	X	
<i>rufida</i>			
<i>spinulifera</i>			
<i>spraguei</i>			
<i>streptacantha</i>	X	X	X
<i>stricta</i>	X		X
<i>tapona</i>		X	
<i>tehuantapecana</i>			
<i>tomentosa</i>			X
<i>undulata</i>			
<i>velutina</i>			
<i>violacea</i>	X		
<i>wilcoxii</i>			
Total	12	8	6

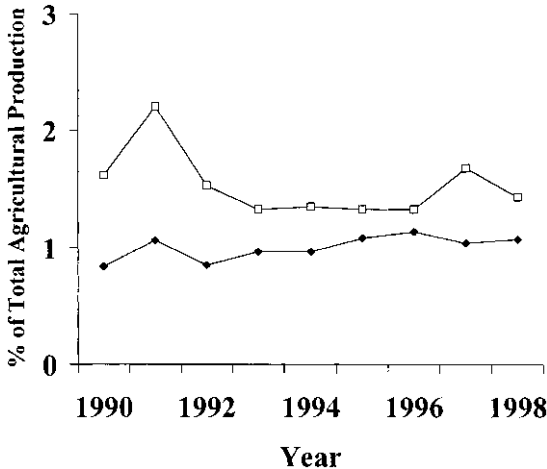


Fig. 1. Percentages of total Mexican agricultural production (closed dots) and value (open dots) of *Opuntia* products occupied by *Opuntia* species between 1990 and 1998.

ern Mexico (Pemberton 1995), we have no direct evidence that it has invaded Mexico to date. However, its movement through the southeastern United States into Mexico is likely.

In order to assess potential impact of *C. cactorum* in Mexico, the second part of this paper presents results of models of possible invasion routes and ultimate distribution.

MODELING INVASION AND DISTRIBUTION OF *C. CACTORUM* IN MEXICO

METHODS

In order to assess the potential invasion and impact of *C. cactorum* on Mexican species of *Opuntia* we used bioclimatic modeling (FloraMap ver. 1.0, Jones & Gladkov 1999) to predict the distribution of *C. cactorum* as well as model the distribution of *Opuntia* species. FloraMap relies on 36 climatic variables and a principal component analysis for prediction. We used the Smithsonian collection to obtain localities of specimens of *C. cactorum*. The distribution of *Opuntia* species was modeled with GARP (Genetic Algorithm for Rule set Prediction; Stockwell & Noble 1991, Stockwell & Peters 1999; <http://biodi.sdsc.edu>) that contains databases for North America only. In these models the ecological requirements of a species are key to the inferential portion of the method. The data points used for bioclimatic modeling of *Opuntia* species were taken from herbaria collections (MEXU, ENCB, SD, XAL) as well from the databases collected by CONABIO (<http://www.conabio.gob.mx>). Species of *Opuntia* with less than three data points were eliminated from further analyses to avoid sampling bias. Distribu-

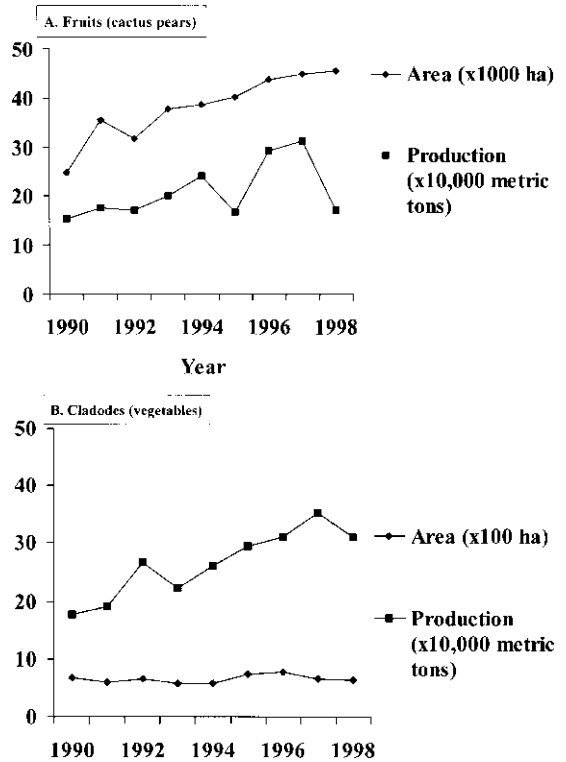


Fig. 2. Production ($\times 10,000$ metric tons) and area ($\times 100$ ha) under cultivation in Mexico of (A) *Opuntia* fruits (cactus pears) and (B) *Opuntia* cladodes (used as vegetables).

tion maps generated by GARP were constrained to ecological regions where *Opuntia* species have been recorded, excluding those areas that were predicted by GARP but lacked the presence of *Opuntia* data points (commission error; Peterson and Cohoon 1999). Overlaying all the predicted maps for *Opuntia* we obtained a map of density of species of *Opuntia*. We predicted the potential risk to all species of *Opuntia* that are found in Mexico by overlapping the richness-of-*Opuntia* maps with the predicted distribution of *C. cactorum*.

RESULTS

Of the 52 species of *Opuntia* evaluated in this study, 15% (8 species) are known to be attacked by *C. cactorum* and an additional 27% (14 species) are taxonomically related to these 8 species (Table 1). At least four species of economic importance (*O. ficus-indica* (L.) Miller, *O. lindheimeri* Engelm., *O. streptacantha* Lemaire and *O. stricta* Haworth) are known to be attacked by *C. cactorum* (Table 1).

The potential distribution of *C. cactorum* includes large parts of the southern and southwestern United States. Since *C. cactorum* is already

present and established in Florida, it will probably be just a matter of time for it to get to the Mexican border. In Mexico, the highest suitability areas are found in the east and northeast, with other areas of high probability in the southeast and along the coastal regions. The predicted distribution of *C. cactorum* suggests a higher probability of invasion through the northern border region than along the southeast as has been previously suggested.

The species having the highest risk (those known to be attacked by *C. cactorum*; Table 1) are located in the eastern border regions of Mexico, and are highly concentrated in central Mexico (Fig. 3). Even though there are species of *Opuntia* (*O. stricta* and *O. lindheimeri*) that overlap with the potential distribution of *C. cactorum*, most of the susceptible species of *Opuntia* are concentrated in central Mexico, where the bioclimatic analysis predicts a lower impact of the moth.

About 20% of the predicted distribution range of species known to be attacked by *C. cactorum* overlaps with adequate habitat for the insect (Table 2). If we consider all species of *Opuntia* evaluated in the analysis, the values of overlap increase to close to 50% (Table 2). The areas in the western part of Mexico show some overlap with potential *C. cactorum* distributions, with only a small portion of *Opuntia* species richness overlapping with the predicted distribution of the insect (Fig. 3).

Little is known of the potential for *C. cactorum* to utilize *Opuntia* species not studied, or of its potential to adapt to or survive in various climates. Therefore, the overlap and impact could possibly be greater than predicted.

DISCUSSION

Mexico and the southwestern United States have a long tradition of use and consumption of *Opuntia* species as well as having the highest di-

versity of *Opuntia* species (Bravo-Hollis & Sánchez-Mejorada 1991) and in Mexico a significant portion of the local and national agricultural economy depends on *Opuntia* resources. Unfortunately, our results suggest that there is a high risk of *C. cactorum* spreading into Mexico from the United States. The establishment of the moth in Mexico is very likely given the large areas of similarity of environmental conditions with those found in its native habitat. The main routes of invasion are concentrated in the northeastern portions of Mexico suggesting a possible invasion through the desert regions of Texas, where species known to be attacked by the cactus moth are present (*O. lindheimeri* and *O. stricta*) and climatic similarity with areas of *C. cactorum* are also found.

The distribution patterns of *Opuntia* species and those predicted for *C. cactorum* show an area of overlap, mainly associated with *Opuntia* species that are susceptible to attack. Although little is known of the potential of *C. cactorum* to adapt to diverse environments, we can assume it to be high, as the moth has been successfully introduced into many areas of the world (Hawaii, the Caribbean region, South Africa and Australia) suggesting that the potential overlap between the insect and native opuntias can increase dramatically. Clearly, diet selection experiments are needed to assess the potential impact of *C. cactorum* on all *Opuntia* species that have not had contact with the moth in order to determine the full potential damage.

The predictions suggest northeastern Mexico as a primary route of invasion, followed by the southeastern areas of Mexico. Efforts towards early detection and containment of the invasion of *C. cactorum* have to concentrate on those two areas of Mexico with special emphasis on areas bordering the species-rich areas of central Mexico. The economic impact that will result from an invasion of the cactus moth cannot be determined

TABLE 2. PERCENTAGE OF LAND AREA WITH *OPUNTIA* SPECIES IN MEXICO AND POTENTIALLY COLONIZED BY *CACTOBLASTIS CACTORUM*. COVERAGES WERE DEVELOPED FROM BIOCLIMATIC MODELING WITH GARP AND FLORAMAP.

Overlap Parameter	Percent of Mexican Territory	
	Species known to be attacked by <i>C. cactorum</i>	Total number of <i>Opuntia</i> spp. found in Mexico
Suitable for <i>C. cactorum</i> , but with no species of <i>Opuntia</i> .	32.51	9.85
Suitable for <i>C. cactorum</i> and with at least one species of <i>Opuntia</i> .	23.75	49.11
Unsuitable for <i>C. cactorum</i> and with at least one species of <i>Opuntia</i> .	12.79	35.99
Unsuitable for <i>C. cactorum</i> and with no species of <i>Opuntia</i> .	28.25	5.05

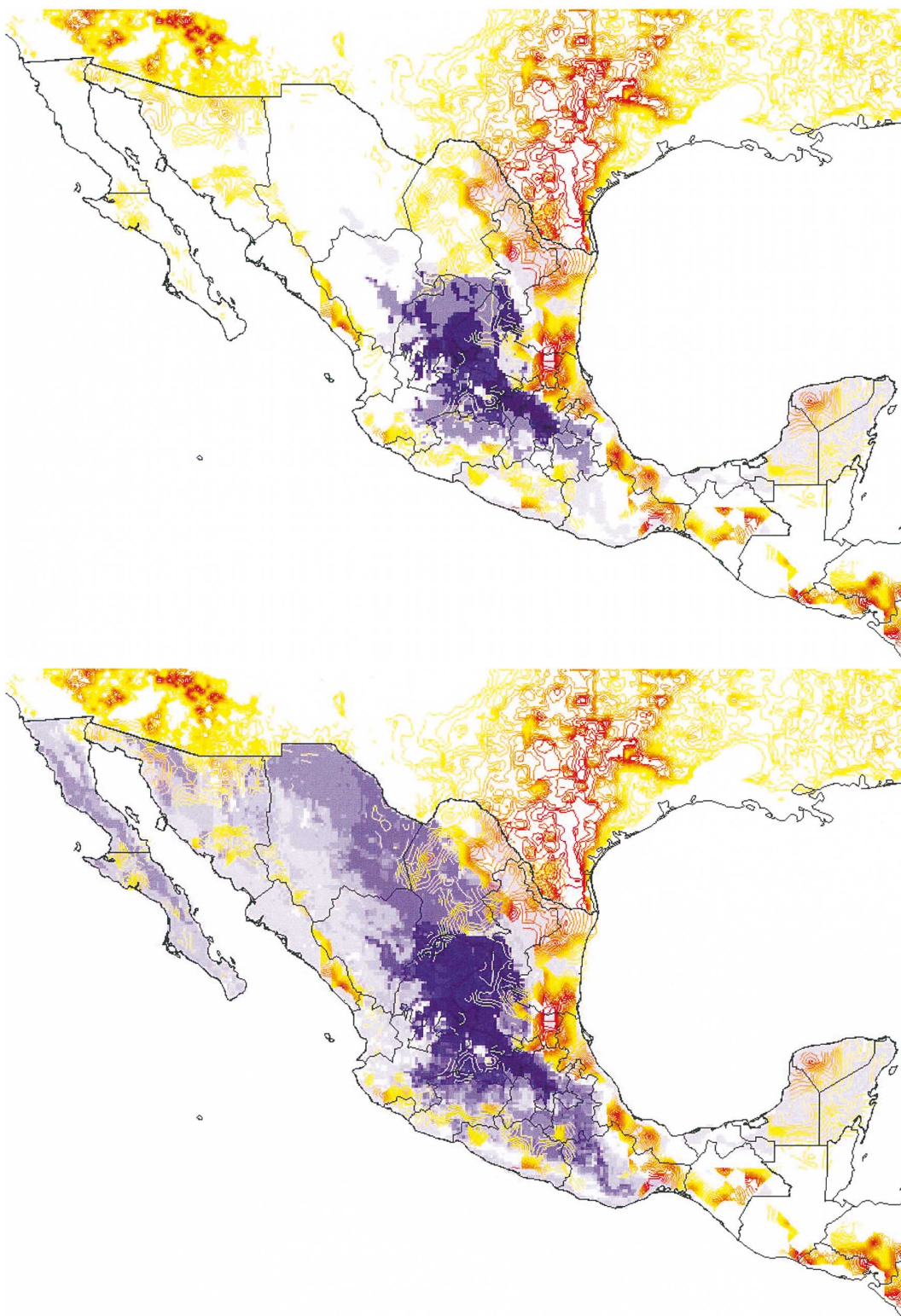


Fig. 3. Overlay of GARP *Opuntia* species distribution predictions (blue) and FloraMap predicted distribution of *C. cactorum* habitat (red). Top: species of *Opuntia* known to be attacked by *C. cactorum*. Bottom: all species of *Opuntia* used in the analysis.

yet, however, given the economic and social importance of *Opuntia* in Mexico we can expect the damage to be significant. Bioclimatic modeling is a valuable tool to predict areas where invasion is likely and can help to provide background information to plan future actions towards mitigating the impact an invasive species such as *C. cactorum* can have on local populations of *Opuntia*.

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REFERENCES CITED

- BARBERA, G. 1995. History, economic and agro-ecological importance, pp. 1-11. In G. Barbera, P. Inglese, and E. Pimienta-Barrios [eds.]. Agro-ecology, cultivation and uses of cactus pear. FAO Plant Production and Protection Paper 132. Rome, Italy.
- BRAVO-HOLLIS, H. H. 1978. Las Cactáceas de México. Vol. 1. Universidad Nacional Autónoma de México, 743 pp.
- BRAVO-HOLLIS, H., AND H. SÁNCHEZ-MEJORADA. 1991. Las Cactáceas de México. Vol 3. Universidad Nacional Autónoma de México, 643 pp.
- CASAS A., J. CABELLO, A. VALIENTE-BANUET, J. A. SER-RANO, AND P. DAVILA. 1999. Morphological variation and the process of domestication of *Stenocereus stellularis* (Cactaceae) in central Mexico. *Am. Jour. Bot.* 86: 522-533.
- COLUNGA-GARCIA MORIN, P., J. COELLO-COELLO, L. E. EGUILARTE, AND D. PIÑERO. 1999. Isozymatic variation and phylogenetic relationships between henequen (*Agave furcroydes*) and its wild ancestor *A. angustifolia* (Agavaceae). *Am. Jour. Bot.* 86: 115-123.
- FLORES-VALDEZ, C. A., AND J. R. AGUIRRE-RIVERA. 1979. El nopal como forraje. Universidad Autónoma Chapingo Press. Texcoco, Mexico.
- FLORES-VALDEZ, C. A., AND C. GALLEGOS. 1993. Situación y perspectivas de la producción de tuna en la región centro norte de México. Universidad Autónoma de Chapingo—CIESTAAM. Chapingo, México.
- GONZALEZ-ESPINOSA, M., AND P. F. QUINTANA-ASENSIO. 1986. Seed predation and dispersal in a dominant desert plant: *Opuntia*, ants, birds, and mammals, In A. Estrada and T. H. Fleming [eds.]. Frugivores and seed dispersal. Dr. W. Junk Publishers, Dordrecht, Netherlands.
- HOFFMANN, W. 1995. Ethnobotany, pp. 12-19. In G. Barbera, P. Inglese, and E. Pimienta-Barrios [eds.]. Agro-ecology, cultivation and uses of cactus pear. FAO Plant Production and Protection Paper 132. Rome, Italy.
- JONES, P. G., AND A. GLADKOV. 1999. FloraMap Vers. 1. A computer tool for predicting the distribution of plants and other organisms in the wild. Centro Internacional de Agricultura Tropical CIAT CD-ROM Series, Cali, Colombia.
- MADUJANO, M. C., J. GOLUBOV, AND C. MONTAÑA. 1987. Dormancy and endozochorous dispersal of *O. rastrera* seeds in the Chihuahuan desert. *Jour. Arid Envir.* 36: 259-266.
- MONTIEL, S., AND C. MONTAÑA. 2000. Vetebrate frugivory and seed dispersal of a Chihuahuan desert cactus. *Plant Ecology* 146: 221-229.
- PEMBERTON, R. W. 1995. *Cactoblastis cactorum* (Lepidoptera: Pyralidae) in the United States: An immigrant biological control agent or an introduction of the nursery industry. *Amer. Entomol.* 41: 230-232.
- PETERSON A. T., AND K. P. COHOON. 1999. Sensitivity of distributional prediction algorithms to geographic data completeness. *Ecological Modeling* 117: 159-164.
- PIMIENTA, E. 1990. El nopal tunero. Universidad de Guadalajara, Guadalajara Jalisco, Mexico.
- RUSSELL, E. C., AND P. FELKER. 1987. The prickly pears (*Opuntia* spp. Cactaceae): a source of human and animal food in semiarid regions. *Economic Botany* 41: 433-445.
- SAGAR (Secretaría de Agricultura, Ganadería y Desarrollo Rural). 1995-1998. Anuario Estadístico de la Producción Agrícola de los Estados Unidos Mexicanos. Centro de Estadística Agropecuaria, México D.F. México.
- SMITH, C. E. 1967. Plant remains, In D. S. Byers, [ed.]. The History of the Tehuacan Valley: Environment and Subsistence. Univ. Texas Press, Austin.
- STOCKWELL D. R. B., AND I. R. NOBLE. 1991. Induction of sets of rules from animal distribution data: a robust and informative method of data analysis. *Mathematics and Computers in Simulation* 32: 249-254.
- STOCKWELL D. R. B., AND D. PETERS. 1999. The GARP modeling system: problems and solutions to automated spatial prediction. *International Jour. of Geographical Information Sci.* 13: 143-158.
- ZIMMERMAN, H., V. C. MORAN, AND J. H. HOFFMANN. 2000. The renowned cactus moth, *Cactoblastis cactorum*: its natural history and threat to native *Opuntia* floras in Mexico and the United States of America. *Diversity and Distributions* 6: 259-269.