

Bioclimatic Model of the Spined Soldier Bug (Heteroptera: Pentatomidae) Using CLIMEX: Testing Model Predictions at Two Spatial Scales¹

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Abstract A bioclimatic model of the polyphagous predator, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae), was developed using CLIMEX software (Hearne Scientific Software, Melbourne, Australia). Calibration distribution was fitted using known distribution records for the United States and Canada, after which the model was used to generate a potential distribution map for the entire world. As expected, potential distribution maps agreed with known distribution records for North America. However, apparent mismatches were found for distributions in Europe, South America, midAfrica, and Southeast Asia. Using historical weather data, CLIMEX "growth indices" (measures of climate suitability for insect development) were compared against multiyear pheromone trap counts in the northern (Indiana) and southern (Florida) United States. Growth index curves did not appear to match pheromone trap data in either location when examined separately by year, location and insect sex. However, a weak relationship was found between trap counts and growth index when data were pooled across years, locations and sex.

Key Words CLIMEX, *Podisus maculiventris*, bioclimatic modeling, climate envelope, climate mapping

Bioclimatic models use information on the known ecological and climatic tolerances of poikilothermic organisms in their native habitats to predict their potential distribution and population levels in other geographical regions (Gullan and Cranston 2005). The 2-fold process typically consists of replicating the known distribution of the target species, usually in its native habitat, to collate data on climatic conditions favorable to the species of interest, as well as stress factors detrimental to its survival (Sutherst et al. 2004). Afterward, the geographical area of interest is extended or a new area is chosen where the target species may be introduced intentionally, as in a biological control agent (e.g., Goolsby et al. 2005), or unintentionally, as in an invasive pest species (e.g., Hoddle 2004) or for foreign exploration for natural enemies (Hoelmer and Kirk 2005). Because quantitative inferences are made between an organism and its environment, a related application of these models is to simulate the effects of different environmental scenarios such as increased irrigation (e.g., Vera et al. 2002) or global warming (e.g., Yeates et al. 1998).

Here we used CLIMEX (Hearne Scientific Software, Melbourne, Australia; Sutherst et al. 2004) as the bioclimatic model. Under the assumption that establish-

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ment in a geographic region signifies tolerance to its climatic conditions, CLIMEX calculates an annual growth index based on responses to temperature, moisture, diapause and light. The growth index is inhibited by stress indices due to excessive cold, heat, dryness or moisture (and sometimes their interactions). The growth index and stress indices are used to calculate an overall "Ecoclimatic Index" (EI) which indicates the potential for population growth as regulated by stresses, unfavorable seasons and factors such as diapause. Therefore, EI encapsulates an overall measure of the potential for population survival in a given locality.

CLIMEX has an extensive publication history (Sutherst et al. 2004, CSIRO 2005 <http://www.ento.csiro.au/climex/bibliography.htm>) and has been used to study not only insects but plants, e.g., the alligator weed, *Alternanthera philoxeroides* (Mart.) Griseb. (Julien et al. 1995); pathogens, e.g., *Pyrenophora semeniperda* (Brittlebank & Adam) Shoemaker, the causal agent of leaf spotting in many annual and perennial grasses (Yonow et al. 2004); and vertebrates, e.g., the cane toad *Bufo marinus* L. (Sutherst et al. 1995). The CLIMEX model was used to estimate the worldwide potential distribution of the Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), with emphasis on Argentina and Australia based on its observed geographical distribution in the Mediterranean (Vera et al. 2002). Key stress factors limiting distribution were cold stress to the north in Europe and by dryness in northern Africa and in the south of Spain and Portugal. A more analytical approach was taken by Sutherst and Maywald (2005) to study inferred temperature and moisture responses of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), in the United States with implications for its spread throughout Australia and New Zealand. Analysis of the mechanisms limiting its spread suggested that the ant could spread further in the west coast of the United States where infestation patterns would differ from those in the East. In Australia and New Zealand, infestation patterns are predicted to be different from those in the United States, with slower growth and lower winter mortality. Here, we use CLIMEX to examine worldwide distribution of a generalist insect predator, the spined soldier bug, *Podisus maculiventris* (Say) (Heteroptera: Pentatomidae), and compare growth index estimates with pheromone trap data in a northern state (Indiana) and a southern state (Florida) in the United States.

Materials and Methods

Parameterizing the model. CLIMEX files for a given species are parameterized by attempting to replicate distribution in a specific locality, preferably the native distribution of the plant or animal (Sutherst et al. 2004). When available, biological data, such as temperature responses, are used instead of model default values. Stresses due to cold, heat, wetness, dryness or their interactions may be adjusted if needed. A species file for *P. maculiventris* was created from the "comfort" template available in CLIMEX, meant to approximate climatic conditions for human comfort. Temperature index parameters were estimated using the laboratory life table data at different constant temperatures (Legaspi and Legaspi 2005a). The target calibration distribution for *P. maculiventris* is problematic because it is an extremely cosmopolitan insect, and distribution records may lack precision or reliability for the purposes of parameter estimation. Distribution records of *P. maculiventris* in the United States and Canada (McPherson 1982) were used to create the target distribution map (see also, Henry and Froeschner 1988, De Clercq 2000).

Analyzing predicted world distribution of *Podisus maculiventris*. Following CLIMEX procedures, when the model distribution approximated that of the target distribution, other areas were examined for potential distribution. The parameter file for *P. maculiventris* was run using the "Compare Locations" function to examine predicted distributions throughout the world. The model used a global climate surface consisting of climatic averages calculated into a 0.5° grid and maintained by the Intergovernmental Panel on Climate Change (IPCC; <http://ipcc-ddc.cru.uea.ac.uk/>), a joint effort of the Climatic Research Unit in the United Kingdom, the Deutsches Klimarechenzentrum in Germany and the Center for International Earth Science Information Network at Columbia University in New York (see IPCC-TGCIA 1999). Potential insect distribution was examined for areas other than North America.

Field data validation of the CLIMEX model. Field data from Indiana were collected near the campus of Purdue Univ. in West Lafayette, IN ($\approx 40^{\circ}22' N$, $86^{\circ}52' W$) from 1987-1989 (described in Legaspi et al. 1996). Field data for Florida were collected at the Center for Viticultural Sciences & Small Fruit Research, FL A&M Univ., Tallahassee, FL ($\approx 30^{\circ}23' N$, $84^{\circ}22' W$) from 2001-2005 (Legaspi et al. 2004, Legaspi and Legaspi 2005b). *Podisus maculiventris* adults were sampled using plastic-covered traps with a glass vial filled with a pheromone mixture (Aldrich 1988) and a cotton wick, as well as a vial of water inserted with a cotton wick. Each trap was made from an inverted plastic food container. Insects entered through a wire screen funnel at the top and were removed through the screw cap lid at the bottom of the trap. The water and pheromone mixture was replaced biweekly or as needed. Samples were collected daily (except weekends) around 1500h, when most adults were observed to be caught. Pheromone trap counts were plotted against corresponding predicted growth index values. A regression analysis was performed on insect trap counts as the dependent variable and growth index as the independent variable using Systat 11 (Systat Software, Inc., Point Richmond, CA).

Results

Parameterizing the model. The lower temperature threshold for development was initially set to 12°C, and the thermal requirement for completion of 1 generation was estimated at 800 degree-days. The target distribution almost completely encompassed the mainland United States, as well as most parts of Canada (Fig. 1, based on McPherson 1982, Henry and Froeschner 1988). Only northern Canada and Alaska had no records of *P. maculiventris*. To approximate this distribution, the developmental threshold was lowered to 8°C. Cold, heat, dry and wet stresses were eliminated from the model, and a liberal soil moisture profile was used (Table 1). The species parameter file was run using world climate data (IPCC-TGCIA 1999). The output map of EI values is shown in Fig. 2.

Analyzing predicted world distribution of *Podisus maculiventris*. The recorded extensive distribution of *P. maculiventris* in North America (McPherson 1982, Henry and Froeschner 1988) resulted in a similar extensive North American distribution in the calibration runs (Fig. 2A). The CLIMEX species parameter file also showed high EI values for South America, midAfrica, Europe (extending to Eastern Europe), Southeast Asia, and the eastern and western coasts of Australia. The insect appears absent only in areas marked by extreme cold, e.g. northern Russian Federation, toward the Polar Regions, or extreme heat, e.g. the Saharan Desert in northern Africa.

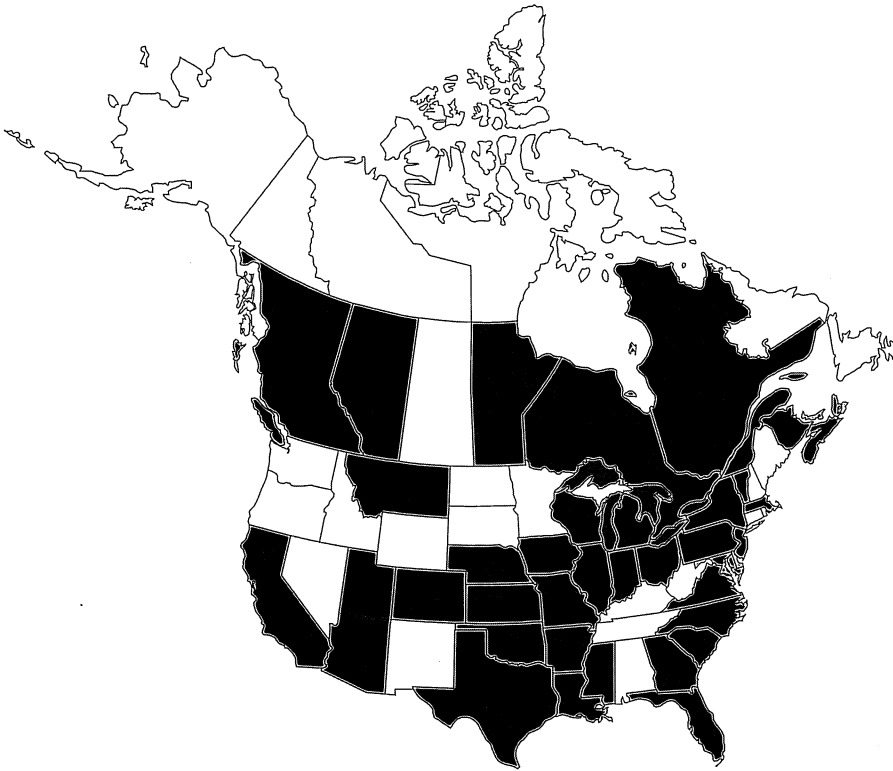


Fig. 1. Target distribution and calibration map of *Podisus maculiventris* in North America (based on McPherson 1982; Henry and Froeschner 1988).

In addition to the U.S. and Canada, the worldwide natural distribution of *P. maculiventris* includes Mexico, the Bahamas, parts of the West Indies, including Haiti and the Dominican Republic (De Clercq 2000, Thomas 1992) (Fig. 2B). *Podisus maculiventris* was introduced as a biological control agent against the fall webworm, *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae), in Korea, Japan and the Yugoslavia. Despite promising levels of control, *P. maculiventris* largely failed to establish, which was attributed to an inability to overwinter, despite the fact that this species can survive winters in the U.S., Canada, Poland, parts of Russia and the Ukraine (De Clercq 2000). The predator was introduced into the European part of the former Soviet Union as a control agent against the Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae). However, establishment appears limited to southern Russia, possibly because of photoperiod effects (see De Clercq 2000). Stamopoulos and Chloridis (1994) report survival and predation rates against *L. decemlineata* in the field in Greece, where the species presumably is established. The prediction that *P. maculiventris* should persist in Europe (here and De Clercq 2002) is contradicted by the failure of classical biological control importations in the 1930s-1970s against *L. decemlineata* into several European countries (e.g., France,

Table 1. CLIMEX species parameter file for *Podisus maculiventris* (temperature and degree day estimates based on Legaspi and Legaspi 2005a; moisture index values based on calibration to target distribution)

Parameter	Description (described in Sutherst et al. 2004)	Value
Temperature Index		
DV0	Lower temperature threshold	8
DV1	Lower optimum temperature	18
DV2	Upper optimum temperature	26
DV3	Upper temperature threshold	34
Moisture Index		
SM0	Lower soil moisture threshold	0.01
SM1	Lower optimal soil moisture	0.2
SM2	Upper optimal soil moisture	2.0
SM3	Upper soil moisture threshold	2.5
PDD	Degree days per generation	800

Germany) using insects from Canada and the northern U.S. A possible explanation for its failure to establish is heavy parasitization by endemic scelionid wasps (e.g., *Trissolcus*, *Telenomus*) (De Clercq 2002).

The potential distribution map in Fig. 2A was calibrated for Canada and the U.S., but also shows climatic matching for Mexico which is supported by independent distribution records (De Clercq 2000, Thomas 1992). South America is predicted as potential distribution for *P. maculiventris*, but we found no records of occurrence in this region. Similarly, no records were found for midAfrica, Southeast Asia and eastern Australia. It is difficult to determine whether the absence of records in these regions is because of climate or other factors, or simply because no records were made. However, we believe the predicted distribution generated by CLIMEX would be reasonable or understandable to most field entomologists familiar with *P. maculiventris* and its climatic thresholds.

Field data validation of the CLIMEX model. CLIMEX data generated for a location with closest coordinates to West Lafayette, IN, were (40°30'N, 86°30' W) and Tallahassee, FL (30°30'N, 84°80'W) (Fig. 3). Pheromone trap counts for Indiana (1987-1989) are superimposed on GI values generated by CLIMEX for the geographical coordinates stated (Fig. 4). Corresponding graphs for Florida are shown in Fig. 4. GI-values for Indiana are roughly bimodal, beginning in May, ending in December, and peaking approximately in June and October. By contrast, GI-values for Florida increase earlier in March, and show a more clearly defined separation of peaks occurring in April and November (Fig. 5). When compared against field phenology data in the form of pheromone trap counts, no correspondence is apparent between weekly GI values and insect counts when graphs are examined by sex, year and location. However, the regression analysis of pooled trap counts and growth

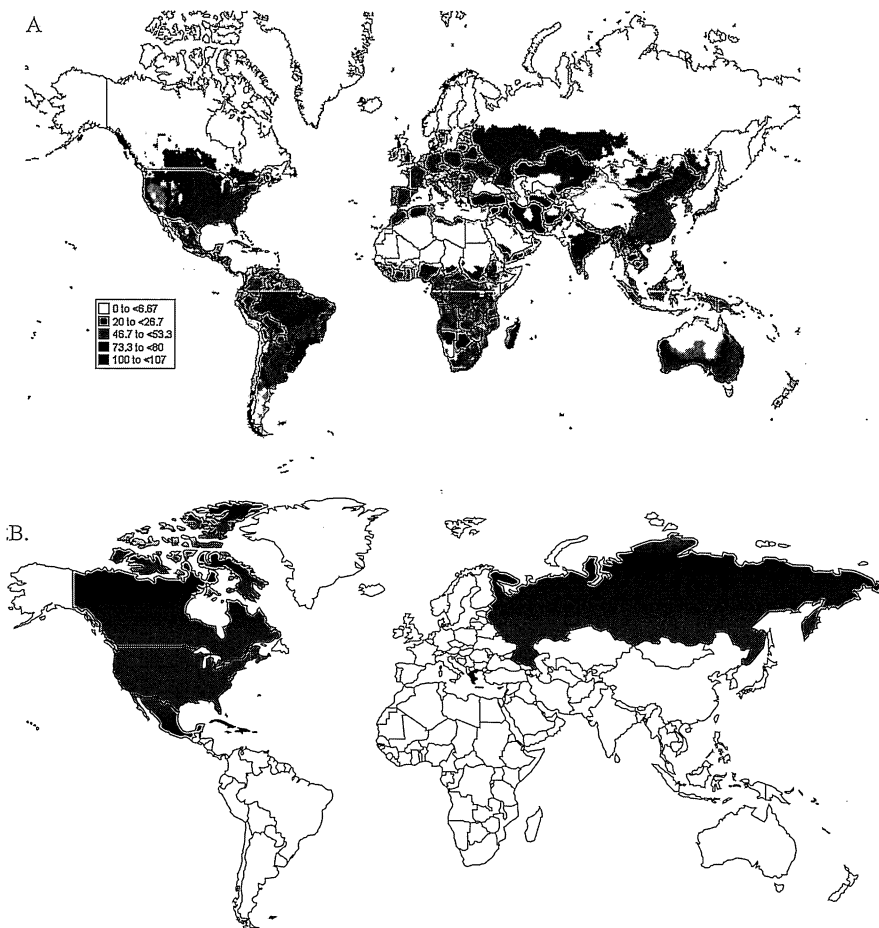


Fig. 2. A) Predicted worldwide distribution based on species parameter file for *Podisus maculiventris* (shading and corresponding EI values indicated in box). B) Approximate actual known distribution of *P. maculiventris*.

indices yielded a significant model: $Y = 0.1225 + 0.925 \text{ GI}$ (SE = 0.094, 0.153, respectively) ($F = 36.7$; $df = 1, 1398$; $R^2 = 0.026$; $P < 0.001$) (Fig. 6). The low R^2 value suggests a weak relationship between pooled trap counts and GI.

Discussion

Limitations of bioclimatic modeling. Bioclimatic models such as CLIMEX assume that the distribution of biological organisms, especially poikilothermic insects, is determined by climate, absent evidence to the contrary (Sutherst et al. 2004). Extending the ecological niche concept of Hutchinson (1957), climate is used to define a "fundamental" (or "physiological") niche into which a species may expand its

CLIMEX Weather Data (IPCC-TGCIA 1999)

- Maximum Temperature
- Minimum Temperature
- Rainfall
- Relative Humidity (3 pm)
- ⋯ Relative Humidity (9 am)

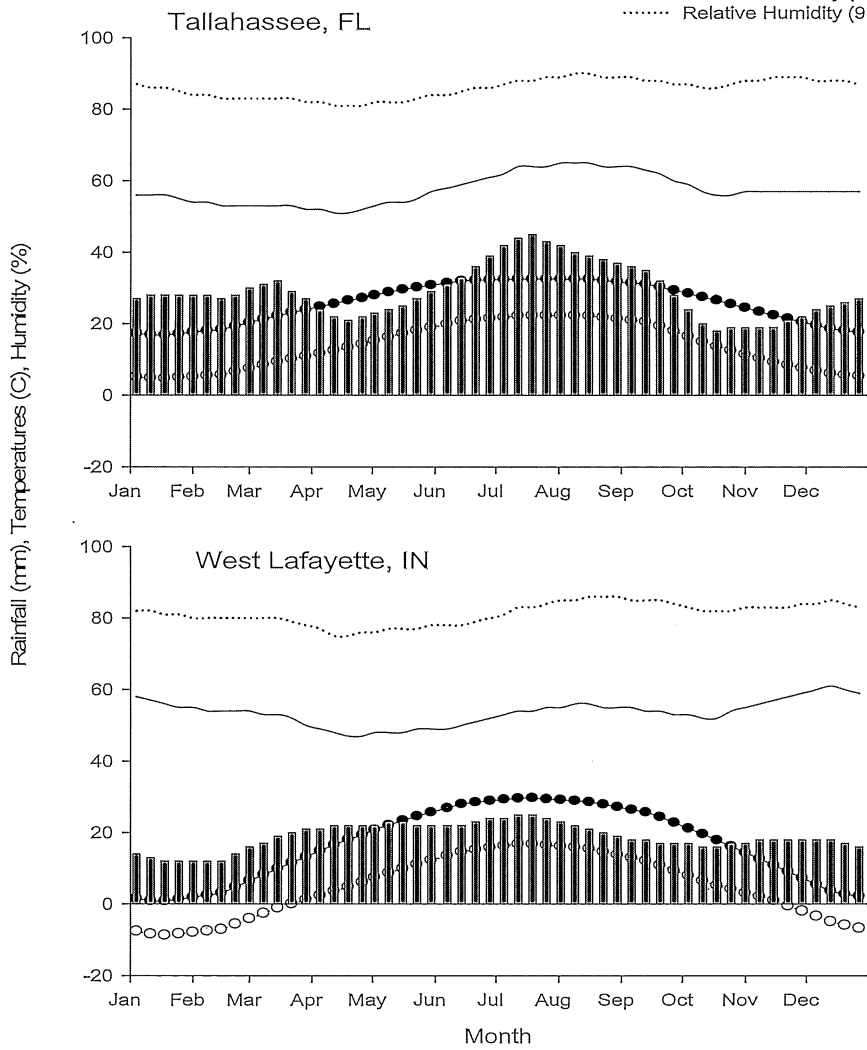


Fig. 3. CLIMEX historical weather data used for West Lafayette, IN and Tallahassee, FL (IPCC-TGCIA 1999).

distribution to a “realized” (or “ecological”) niche, depending on other nonclimatic factors (see Soberón and Peterson 2005). The validity and utility of climate matching has been the subject of controversy. It has been criticized as a fundamentally flawed method (e.g., Davis et al. 1998a, b, Lawton 1998), which in turn has drawn others to its defense (e.g., Hodkinson 1999, Baker et al. 2000). Clearly, distribution of organ-

Growth Index and Field Counts of *Podisus maculiventris* (Indiana, 1987 - 1989)

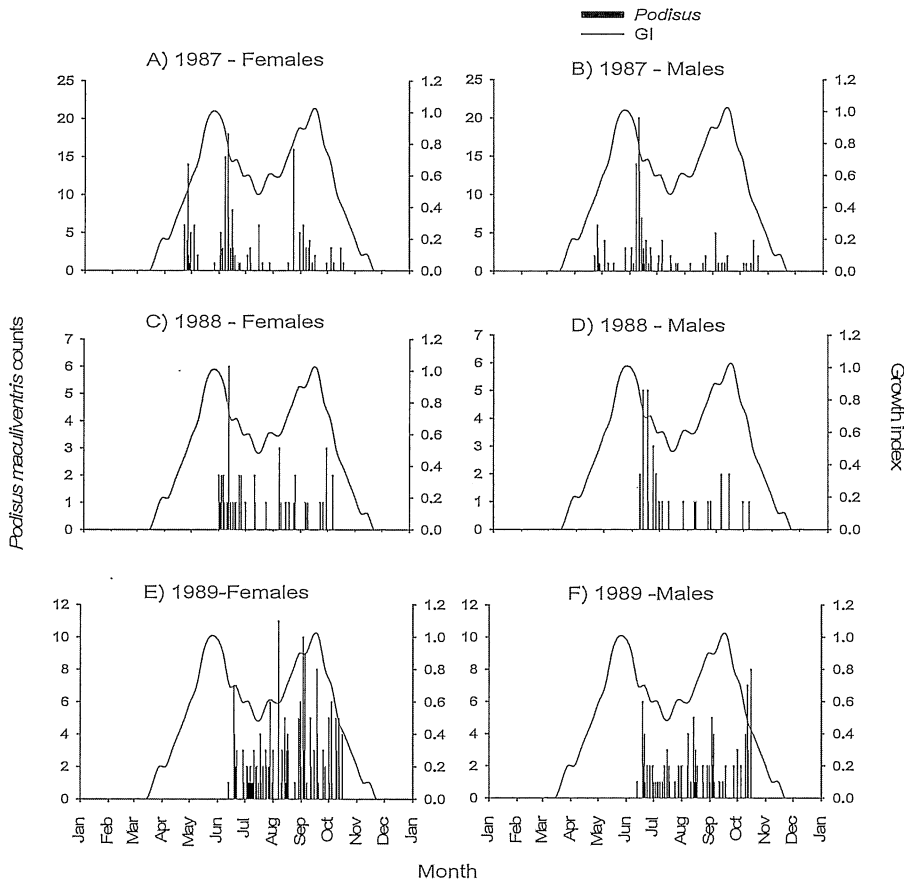


Fig. 4. Cumulative trap counts of *Podisus maculiventris* adults collected in Indiana (1987-1989; methods in Legaspi and Legaspi 2005a, Legaspi et al. 1996) divided by sex. Growth index curve calculated using CLIMEX for the approximate geographical coordinates is superimposed.

isms is determined by factors other than climate. Pearson and Dawson (2003) cite three general nonclimatic factors that affect species distribution:

1. Biotic interactions: Both horizontal (e.g., competition) and vertical (e.g., enemy-victim) trophic interactions can affect the range and distribution of a given species (Davis et al. 1998a, b, Jiang and Morin 2004, Pearson and Dawson 2003, Case et al. 2005). In thermal clines maintained within a series of incubators, interactions among three species of *Drosophila* and a parasitoid resulted in different distributions compared with those of single species (Davis et al. 1998a, b). Therefore, when potential distributions estimated by CLIMEX conflict with observations, biotic

interactions is a plausible explanation. For example, estimated potential distributions of the Mediterranean fruit fly agreed with observed data in Argentina and historical data in Australia, but not with current distribution in eastern Australia (Vera et al. 2002). These discrepancies were attributed to competitive displacement by the Queensland fruit fly, *Bactrocera tryoni* (Froggatt) (Tephritidae). Other biotic interactions include hybridization (Sutherst and Maywald 2005), availability of food and synchrony with hosts (Baker et al. 2000).

2. Rapid evolutionary change. Rapid local evolution has been shown to occur in natural systems, causing changes in geographic distributions, with or without concurrent environmental change (Parmesan et al. 2005). Evolutionary change increased the geographical distributions of four insect species over the past 20 yrs in Britain (Thomas et al. 2001). The butterflies, *Hesperia comma* (L.) (Lepidoptera: Hesperidae) and *Aricia agestis* (Denis & Schiffermüller) (Lycaenidae), increased the number of habitats they could colonize, whereas the bush crickets, *Conocephalus discolor* Thunberg (Orthoptera: Tettigonidae) and *Metrioptera roeselli* Hagenbach showed increased proportions of longer-winged and therefore more dispersive adults in their populations. When CLIMEX was used to predict the geographical range potential of the glassy-winged sharpshooter, *Homalodisca coagulata* (Say) (Hemiptera: Cicadellidae) and the grape pathogen *Xylella fastidiosa* (Hoddle 2004), the model predicted geographical limits imposed by cold stress accumulation in France and parts of Spain and Italy, contrary to reported distributions in Kosovo. The anomaly was attributed to the development of cold-tolerant strains of the bacterium (Hoddle 2004).
3. Species dispersal. The effect of dispersal on distribution is that it uncouples dependence on local climate and allows populations to persist in suboptimal environments and occupy larger ranges than suggested by physiology (Davis et al. 1998b), i.e., the “rescue effect” (see also Fahrig and Jonsen 1998, Travis et al. 2005). In a changing environment, adequate dispersal ability is needed to keep pace with climatic change (Pearson and Dawson 2003). Successful dispersal in response to climate change is dependent not only on biological attributes, but also on factors such as human-mediated transport, or physical barriers to dispersion and habitat fragmentation which act as impediments (Case et al. 2005). The CLIMEX study on fire ant distribution by Sutherst and Maywald (2005) discusses possible effects of physical barriers (habitat types), vectors and artificial environment (e.g., nurseries) on ant dispersal.

Model validation—macro scale. The problems we encountered in collecting data to both calibrate and validate the CLIMEX model are likely to be typical for most scientists attempting similar studies. Detailed distribution records were difficult to obtain, despite the fact that *P. maculiventris* is a well-documented insect. We need to determine definitively whether the absence of records from large regions such as Southeast Asia or South America is because sampling was performed, but no *P. maculiventris* were collected, or simply because no sampling efforts were undertaken. In other words, absence data is almost as important as presence data (Soberón and Peterson 2005). Furthermore, the known distribution of a species may be envisioned as the intersection set of potential distributions due to abiotic factors, biotic factors, and ecological “accessibility” (e.g., barriers to movement and colonization). In the case of South America, it is doubtful that colonization and establishment of *P. maculiventris* were hindered by lack of appropriate prey because it is highly polyphagous

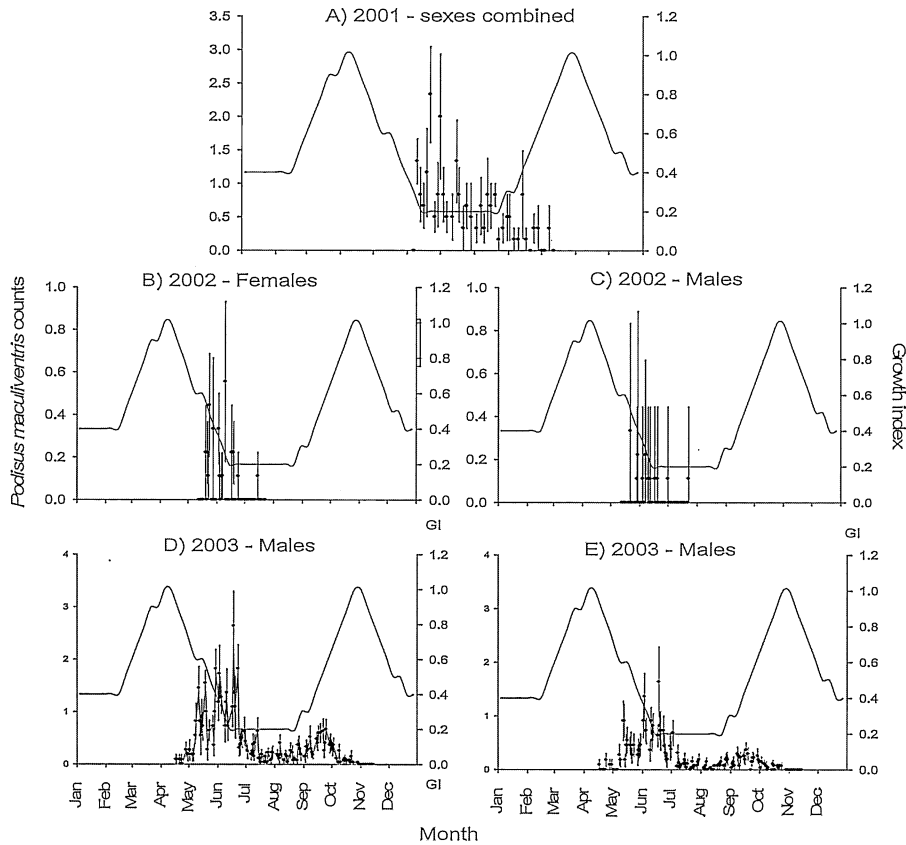
Growth Index and Field Counts of *Podisus maculiventris* (Florida 2001-2005)

Fig. 5. Cumulative trap counts (mean \pm SE) of *Podisus maculiventris* adults collected in Florida (2001-2005; methods in Legaspi and Legaspi 2005b) divided by sex (except for 2001). Growth index curve calculated using CLIMEX for the approximate geographical coordinates is superimposed.

(McPherson 1980). It is interesting to speculate on the possibility that its ecological niche has been occupied by closely related species such as *P. rostralis* (Stål) and *P. nigrispinus* (Dallas), present in Brazil (e.g., Zanuncio et al. 2002); in contrast to *P. maculiventris* which is known to be absent in that country (J. C. Zanuncio, pers. comm.).

In addition to problems with distribution record data, weather data may not be available for specific times and locations of interest. We used climatic averages provided by IPCC-TGCI (1999) which produced identical GI curves not specific to the years sampled. Climatic data specific to Tallahassee and West Lafayette during the years sampled may provide better matches between simulations and field data. However, it may be difficult to correctly scale weather data and insect physiology parameters to sampling areas (Baker et al. 2000).

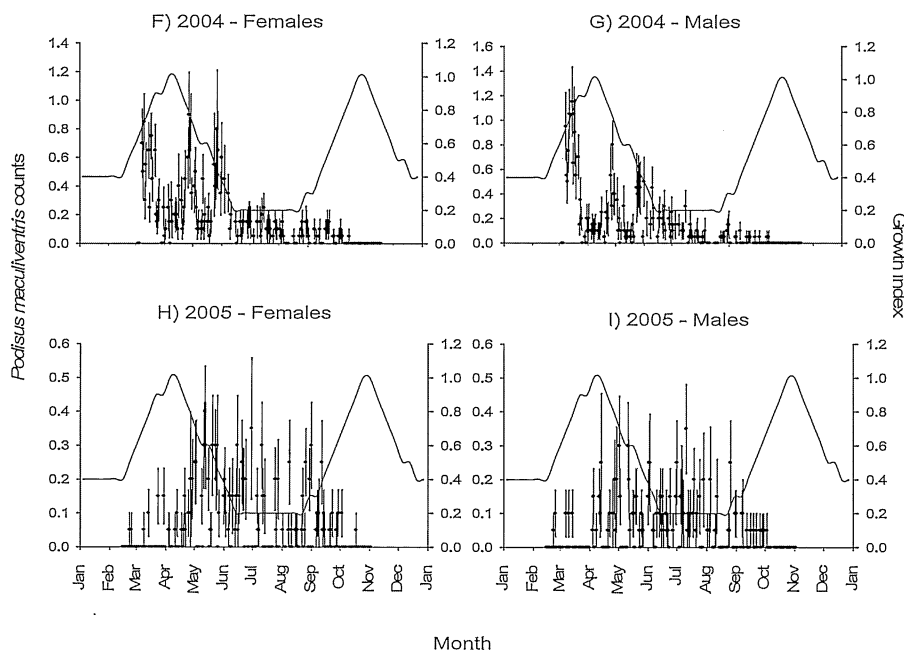


Fig. 5. Continued.

Insect physiology data needed to parameterize CLIMEX models assume uniform values for a given species, irrespective of geographical location. In an insect as cosmopolitan as *P. maculiventris*, a potentially significant complication is that strains of different geographical origins have differing bionomics perhaps as adaptations to local climate (De Clercq 2000). Nymphal development times for strains originating from the southern U.S. (Florida) were shorter than those from the north (New York).

Model validation—micro scale. We used our best available insect census data, in the form of weekly pheromone trap counts, to attempt to validate seasonal growth index curves generated by CLIMEX. There are obviously many limitations to this approach. For example, we did not record immature stages. The growth index is an estimate of the degree to which climatic conditions are favorable for insect development, and may be poorly correlated to adult counts. At the very least, there should be a time delay between development and pheromone trap count. The low R^2 value (0.026) between pooled trap counts and growth index suggests a weak relationship between the two factors. Therefore, despite the apparent inconsistent relationship between GI and trap counts on an intrayear basis, data pooled over many years and locations can indicate a weak positive relationship between GI and trap counts. A stronger correlation should be achieved between GI-values derived using time- and location-specific weather data, against insect field data comprised of measures of immature development such as length and weight. This study currently is close to completion (JCL, unpubl. data).

Rafoss and Sæthre (2003) also compared pheromone trap counts of the codling

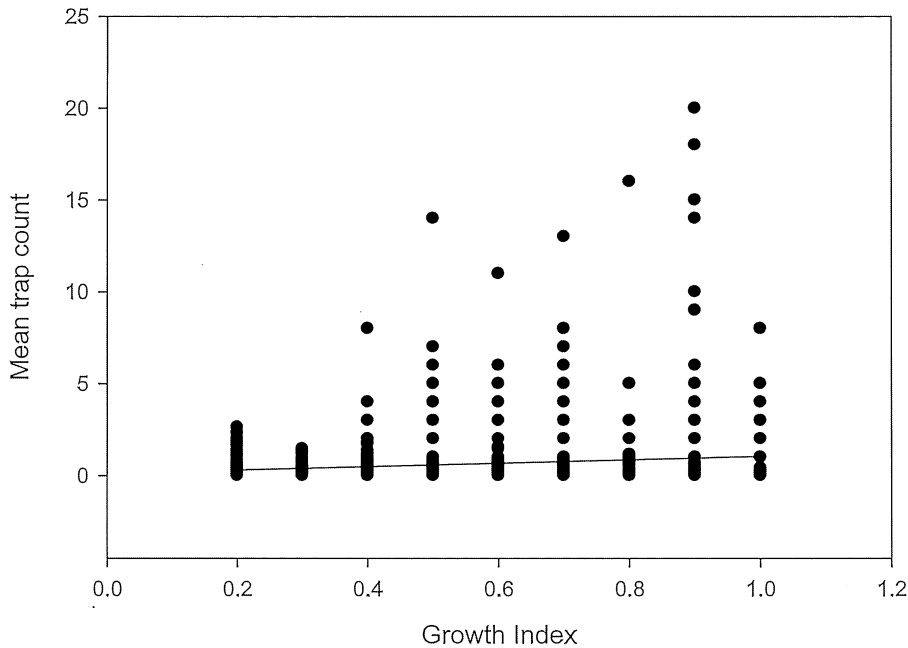


Fig. 6. Regression of pooled trap counts against corresponding growth index at time of sampling. Data were pooled for all years, both sexes and both states. The regression equation is: $Y = 0.1225 + 0.925GI$ (SE = 0.094, 0.153, respectively) ($F = 36.7$; $df = 1, 1398$; $R^2 = 0.026$; $P < 0.001$).

moth, *Cydia pomonella* (L.) (Lepidoptera: Tortricidae), in Norway against CLIMEX ecoclimatic and growth indices. No statistical analyses were performed, although there does not appear to be any relationship among the trap counts and the indices (Rafoss and Sæthre 2003; Fig. 2, p. 81). These workers further caution that pheromone trapping may not provide accurate measurements of population densities, and that insect counts are affected by several factors, including temperature, moonlight, wind speed, and trap or lure placement.

Use bioclimatic models with caution. Despite numerous valid criticisms against the climate matching approach, we believe such models have a useful function in ecology. Even critics of the approach accept that climate models may be useful as "first approximations" (Pearson and Dawson 2003) or "null models" of species distributions (Davis et al. 1998a, b, Lawton 1998). In the absence of appropriate data, climate matching may be the only viable option to predict species distributions (Baker et al. 2000). In this study, we believe that global predictions of *P. maculiventris* distribution would be similar to those that would have been made even without the use of a bioclimatic model. Mismatches in global distribution may be due to biotic factors, accessibility or the absence of sampling efforts. At the field level scale, mismatches between growth index curves and trap counts at given years and locations may be attributed to the diminished role of climate at the local scale. However, pooling the

data across all years and locations suggests a weak relationship may exist between trap count and growth index. Pearson and Dawson (2003) proposed spatial scales at which different environmental factors exerted the strongest effects: climate > topography > land use > soil type > biotic interactions from global (>10000 km) to micro (<10 m), respectively. Our results appear to support this conclusion. Caution should be used when attempting to make field level decisions based on CLIMEX-generated output, at least for specific years. Finally, computer models such as CLIMEX can be used by entomologists and other scientists to serve many purposes, i.e., to define problems, organize thoughts, understand available data and identify data gaps, communicate and test understanding, make predictions, generate hypotheses and act as standards for scientific comparison (Worner 1991). This study presents yet another example that ecology is a difficult science in which to make predictions (Lawton 1998), and of all the functions that computer models perform, they are perhaps poorest at making predictions (Worner 1991).

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