

The North American Invasion of the Giant Resin Bee (Hymenoptera: Megachilidae)

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Abstract.—The giant resin bee, *Megachile sculpturalis* Smith (Megachilidae: Megachilinae), is a species originally of Asia recently adventive in North America. This large and conspicuous species was first recorded at a few localities in the mid-Atlantic states of the United States, but is now found from southeastern Canada (Ontario) to Georgia, and as far west as western Pennsylvania and northwestern Alabama. Known occurrences of this species in its native distributional areas were used to generate an ecological niche model for the species, which can be used to anticipate the geographic potential for species in novel landscapes. The niche model was tested on the native range of the species for robustness in predicting independent suites of occurrence points. The niche model was then used to predict the potential distribution of *M. sculpturalis* in North America—our results indicate that this species has the potential eventually to occupy the entire eastern half of the continent, as far west as the Great Plains. The model also predicts that the species would find appropriate conditions along the Pacific Coast, in Mexico, and in the West Indies. Impacts of *M. sculpturalis* on native *Megachile* species are entirely unknown.

As the most significant and efficient pollinators of flowering plants, bees are critical for many aspects of the diversity and stability of both natural and agricultural ecosystems; in addition, honey bees have long been appreciated for their products (e.g., honey and wax; Michener 2000). These beneficial features make it difficult to think of bees as threats when introduced into areas outside their native ranges, despite the widely known negative effect of exotic species in general (Goulson 2003, Lawton and Brown 1986, Williamson 1999, NAS 2002, Perrings *et al.* 2002).

Several bee species have been introduced into novel regions by man, either deliberately or not. The most famous example is the western honey bee *Apis mel-*

lifera Linnaeus native to Africa, Europe, the Middle East, and northwestern Asia (Ruttner 1988), now globally distributed as human colonists have transported bee colonies. A famous episode in the presence of honey bees in the Americas was the experimental introduction in 1957 of the African *A. mellifera scutellata* Lepeletier de Saint Fargeau ("Africanized" honey bees) into Brazil, and the later establishment of feral populations throughout South and Central America, reaching the southern United States (Kerr 1957, 1967, Michener 1975, Taylor 1977, Sheppard and Smith 2000). Goulson (2003) mentioned other bee introductions carried out to improve pollination, among the most significant, species of the genera *Bombus*, *Me-*

gachile, *Osmia* and *Nomia*. Ascher (2001) mentioned the presence of 17 adventive bee species in North America, providing taxonomic, geographic and biological information for *Hylaeus* (*Spatulariella*) *hyalinatus* Smith, and occurrence notes for *Anthidium* (*Anthidium*) *manicatum* (Linnaeus), *A.* (*Proanthidium*) *oblongatum* (Illiger), *Hoplitis* (*Hoplitis*) *anthocopoides* (Schenck), *Chelostoma* (*Gyrodromella*) *rapunculi* (Lepeletier de Saint Fargeau)¹, *C.* (*Foveosmia*) *campanularum* (Kirby), and (our subject herein) *Megachile* (*Callomegachile*) *sculpturalis* Smith.

The giant resin bee, *M. sculpturalis*, is a robust bee widely distributed in eastern Asia (China, Japan, Taiwan, and Korea). The species is easily differentiated from native North American *Megachile* by its elongate (14–19 mm in males, 22–27 mm in females) parallel-sided body, black head, and dark mesosoma with fulvous setae (Mangum and Brooks 1997) (Fig. 1). It nests preferentially in shady places, a minimum of 0.5 m above the ground, in a variety of cavities, e.g., dry, hollow horizontal stems (bamboo in its native range), and empty burrows made by other hymenopterans (Iwata 1933, Okada 1995), including abandoned wood burrows of carpenter bees (Piel 1933). This latter behavior has already been documented in North American populations (Mangum and Brooks 1997). Brood cells are made of resin from conifers (Iwata 1933) and maple gum (Piel 1933), from which the name “giant resin bee” derives (Batra 1998). In Japan, its period of adult activity is from late June through September (Iwata 1933), coinciding with the blooming of kudzu [*Pueraria lobata* (Willdenow) Ohwi (Leguminosae)], its principal source of pollen (Batra 1998), although it is known to be

polylectic (Mangum and Brooks 1997). Combining the records reported by Batra (1998), Ascher (2001), and Mangum and Sumner (2003), in North America, *M. sculpturalis* has been recorded foraging on flowers of at least 16 plants of 12 families, the most commonly visited being everlasting pea, *Lathyrus latifolius* Linnaeus (Leguminosae); Japanese pagoda, *Sophora japonica* Linnaeus (Leguminosae); privet, *Ligustrum lucidum* W. T. Aiton (Oleaceae); and golden-rain tree, *Koelreuteria paniculata* Laxmann (Sapindaceae), the first native to Europe and the remainder to Asia. Female *M. sculpturalis* leave a trace of their foraging activity on flowers of everlasting pea and Japanese pagoda by puncturing the standard petal (Mangum and Sumner 2003).

In the last decade, *M. sculpturalis* has appeared in eastern North America, with populations established and spreading from their initial areas of appearance (probably near Baltimore, accidentally introduced, via cargo from Japan or China; Batra 1998, Mangum and Brooks 1997). *Megachile sculpturalis* was first collected in North America in 1994 on the campus of North Carolina State University, and by 1996 was widespread in North Carolina (Mangum and Brooks 1997), also reaching Delaware (Mangum and Sumner 2003). It has since spread over much of eastern North America, with records as far west as Athens, Limestone Co., Alabama, as far south as Auburn, Lee Co., Alabama (Kondo *et al.* 2000), and as far north as Onondaga Co., New York (Ascher 2001), and Ontario, Canada (Mangum and Sumner 2003). Records also exist from Georgia, South Carolina, Virginia, Maryland, Pennsylvania, West Virginia, Ohio, Washington D.C., Tennessee, and Connecticut (Mangum and Sumner 2003). Batra (1998) predicted, based on its Asian range, that *M. sculpturalis* would come to inhabit the humid, subtropical to temperate climates of the southeastern and mid-Atlantic Unit-

¹ This species has often been referred to by the older, but preoccupied, name of *C. fuliginosum* (Panzer) (a junior primary homonym in *Apis*), which was replaced by *C. nigricorne* (Nylander), but this itself is a synonym of *C. rapunculi*.

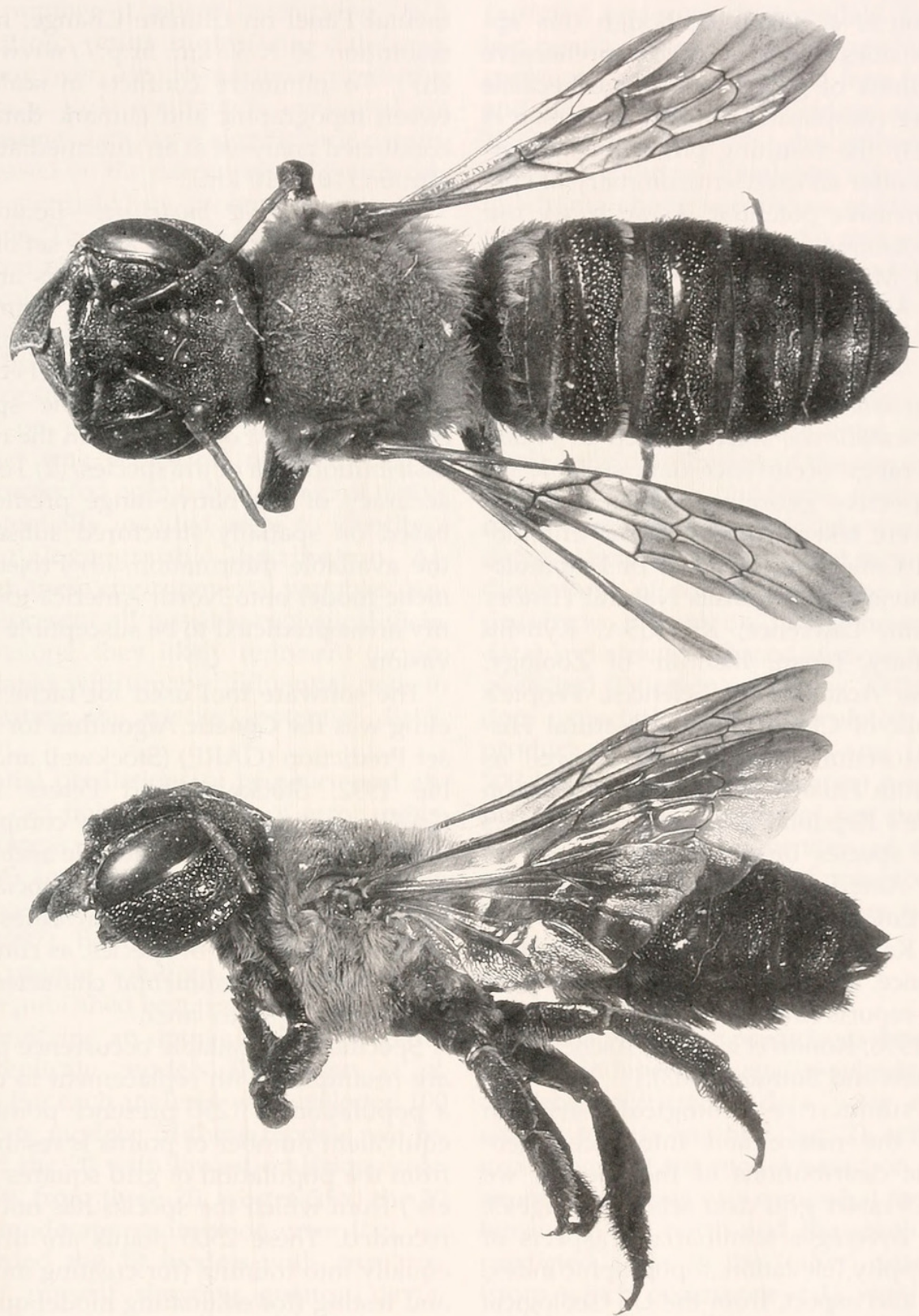


Fig. 1. *Megachile sculpturalis* Smith, female from Japan, above dorsal habitus, below lateral habitus.

ed States, from eastern Texas and Florida, north to southern New England.
Herein we have applied methods of ecological niche modeling. Extensive previous studies have indicated that native-

range ecological characteristics provide excellent predictivity regarding invaded-range ecological and geographic potential of species (Scott and Panetta 1993, Sutherland *et al.* 1999, Skov 2000, Zalba *et al.* 2000,

Peterson *et al.* 2003). Although this approach does not provide comprehensive predictions of geographic range because of other complicating factors (Peterson *et al.* 2003), the resulting predictions nevertheless offer an excellent summary of species' invasive potential. As such, we use this technique to predict the potential extent of *M. sculpturalis*' invasive range in North America.

METHODS

Input data.—Collections with specimens of *M. sculpturalis* were studied to obtain native-range occurrence data suitable for retrospective georeferencing. Specimen data were taken from the Snow Entomological Collection, Division of Entomology, University of Kansas Natural History Museum, Lawrence, KS, USA; Kyushu University, Japan; Institute of Zoology, Chinese Academy of Sciences, People's Republic of China; and the Natural History Museum, London, UK; as well as data from Huan-li Xu personal collection (People's Republic of China). Occurrences of the species on its invaded range in North America were gathered from the Snow Entomological Collection, University of Kansas Natural History Museum, Lawrence, KS, USA, and from recent published reports (Mangum and Brooks 1997, Batra 1998, Kondo *et al.* 2000, Ascher 2001, Mangum and Sumner 2003).

To summarize ecological variation across the native and introduced geographic distributions of the species, we used 15 raster grid data sets ('coverages'). These coverages summarized aspects of topography (elevation, topographic index, slope, and aspect, from the US Geological Survey's Hydro-1K data set, native resolution 1×1 km: <http://edcdaac.usgs.gov/gtopo30/hydro/>) and climate (annual means of diurnal temperature range; frost days; precipitation; maximum, minimum and mean monthly temperatures; solar radiation; wet days; and vapor pressure; for 1960–1990 from the Intergovern-

mental Panel on Climate Change, native resolution 50×50 km: <http://www.ipcc.ch/>). To minimize conflicts in scale between topographic and climatic data, we conducted analyses at an intermediate resolution (10×10 km).

Ecological niche modeling.—Ecological niches are herein defined as the set of conditions under which a species is able to maintain populations without immigration (Grinnell 1917, 1924). Our approach consisted of three steps. (1) Model ecological niche requirements of the species based on known occurrences in the native distribution area of the species. (2) Test the accuracy of the native-range predictions based on spatially structured subsets of the available information. (3) Project the niche model onto North America to identify areas predicted to be susceptible to invasion.

The software tool used for niche modeling was the Genetic Algorithm for Rule-set Prediction (GARP) (Stockwell and Noble 1992, Stockwell and Peters 1999). GARP uses an evolutionary-computing approach to carry out a flexible and powerful search for non-random associations between environmental variables and known occurrences of species, as contrasted with the environmental characteristics of the overall study area.

Specifically, available occurrence points are resampled with replacement to create a population of 1250 presence points; an equivalent number of points is resampled from the population of grid squares ('pixels') from which the species has not been recorded. These 2500 points are divided equally into training (for creating models) and testing (for evaluating model quality) data sets. Models are composed of a set of conditional rules developed through an iterative process of rule selection, evaluation, testing, and incorporation or rejection. First, a method is chosen from a set of possibilities (e.g. logistic regression, bioclimatic rules, etc), and applied to the training data set. Then, a rule is developed

by a number of means (mimicking DNA evolution: point mutations, deletions, crossing over, etc.) to maximize predictive accuracy. Rule accuracy is evaluated via the testing data, as a significance parameter based on the percentage of points correctly predicted as present or absent by the rule. The change in predictive accuracy from one iteration to the next is used to evaluate whether a particular rule should be incorporated into the final rule-set. The algorithm runs either 1000 iterations or until addition of new rules has no effect on predictive accuracy. The final rule-set (the ecological niche model) is then projected onto a digital map of native or potentially invaded areas to identify a potential geographic distribution. Although these environmental variables cannot represent all possible ecological-niche dimensions, they likely represent (or are correlated with) many influential ones in delineating the species' potential distribution.

Spatial predictions of presence and absence can hold two types of error: omission (areas of known presence predicted absent) and commission (areas of known absence predicted present) (Fielding and Bell 1997). Because GARP does not produce unique solutions, we followed recently published best practices approaches to identifying an optimal subset of resulting replicate models (Anderson *et al.* 2003). For each analysis, we developed 100 replicate models; of these models, we retained the 20 with lowest omission error. Finally, from these 20, we retained the 10 with moderate commission error (i.e., we discarded the 10 models with area predicted present showing greatest deviations from the overall median area predicted present across all models). This 'best subset' of models was summed to produce final predictions of potential distributions.

To validate our model predictions, we evaluated their ability to predict independent sets of test points compared with that

expected under random models. Because test results depend critically on how occurrence points are divided into training and testing data sets (Fielding and Bell 1997), we used a 2×2 checkerboard approach (splitting available points into quadrants above and below median latitude and median longitude) that presents a maximum challenge to the model—prediction into broad areas from which no occurrence information was available (Peterson and Shaw 2003). Ecological niche models based on localities in two of the quadrants ('on-diagonal') were used to predict the distribution of the occurrences in the other two quadrants ('off-diagonal'), and vice versa. Models were validated via chi-square tests that incorporate dimensions of correct prediction of both presences (based on independent test data) and absences (based on expected frequencies) (Peterson and Shaw 2003). Random expectations were calculated as the product of the proportional area (within 500 km of known occurrences) predicted present and the number of test presence points. Observed frequencies of correct and incorrect predictions of presence were then compared with expectations using a χ^2 test (1 df).

RESULTS

The native-range predictions based on the two independent spatial subsets of the available occurrence data were closely similar to one another (Fig. 2), with the exception that the model based on on-diagonal quadrants was somewhat more extensive in the north and the south. Both predicted areas in the 'other' quadrants (from which occurrence data were withheld from the modeling exercise) that coincided well with the test points in those areas (both $\chi^2 > 23.90$, both $P < 10^{-1.01414}$). Although the two reciprocal predictions are not identical, their substantial significance nonetheless indicates clear predictive ability of our models for distributional phenomena related to this species.

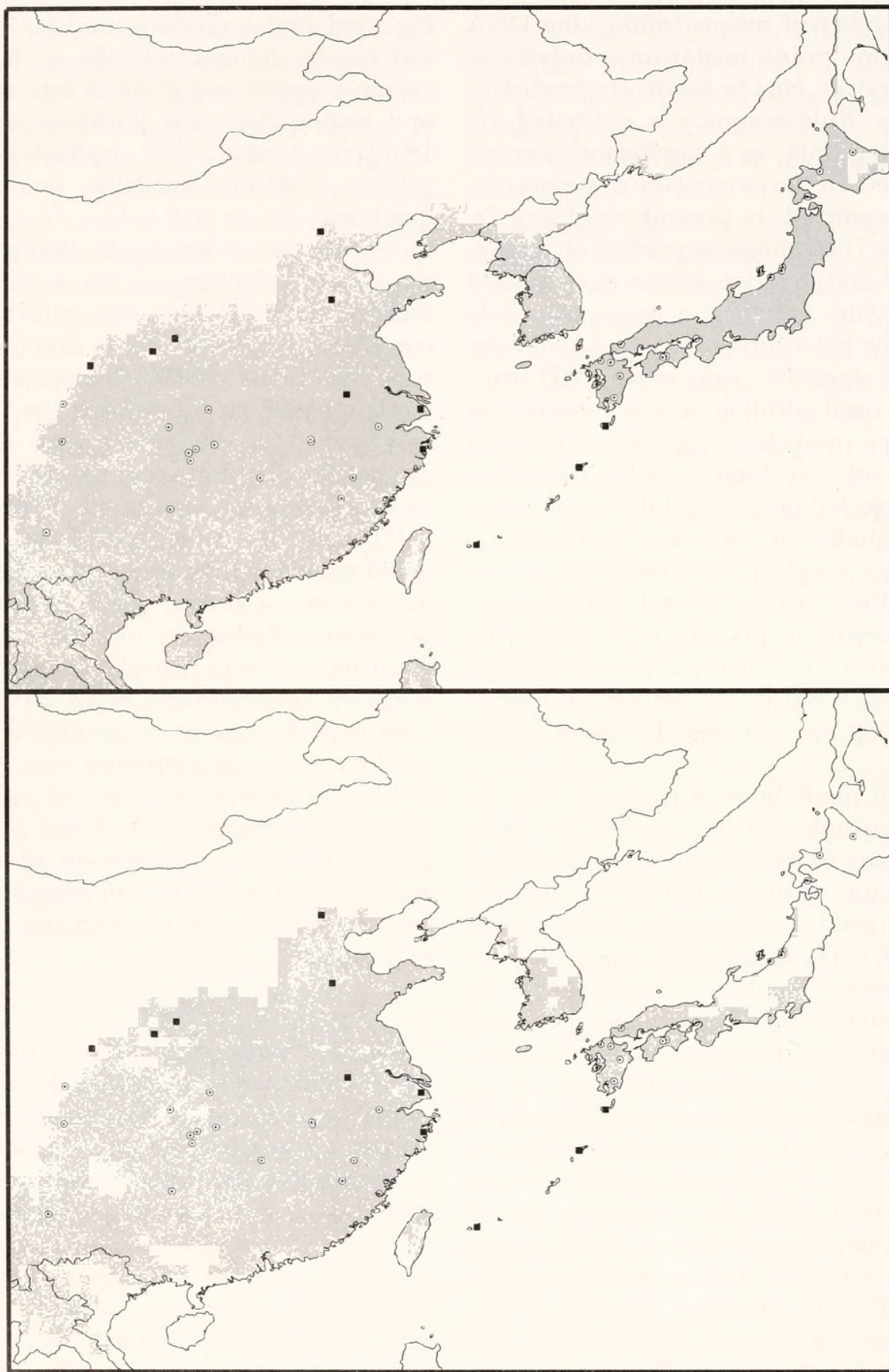


Fig. 2. Predictions of native geographic distribution of *Megachile sculpturalis* Smith, based on two distinct subsets (here depicted as squares versus circles) of the available data—on-diagonal quadrants predict off-diagonal quadrants (top), and vice versa (bottom).

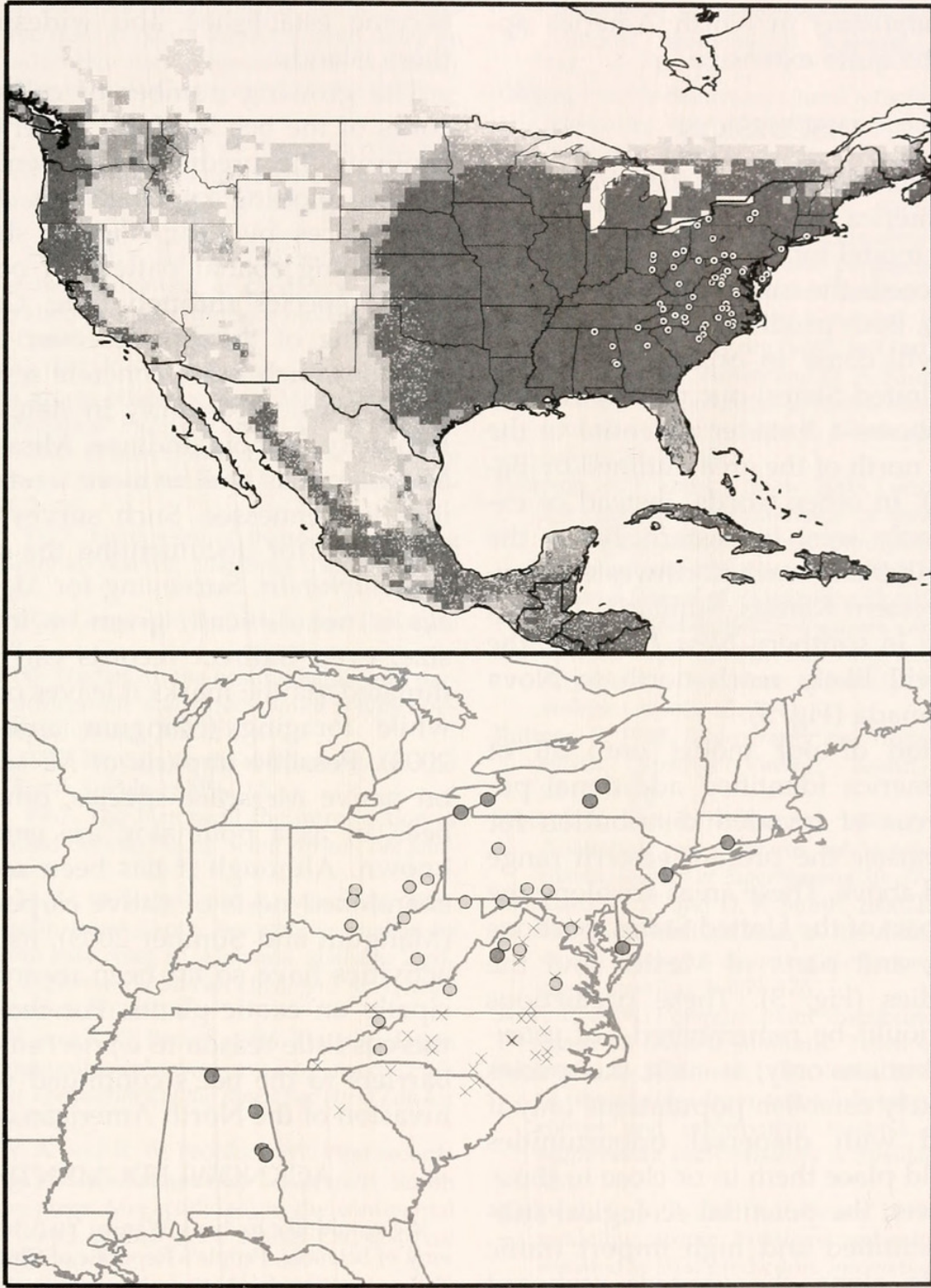


Fig. 3. Projection of native-distribution ecological niche model for *Megachile sculpturalis* Smith to the United States, identifying areas putatively suitable for the species (top); observed pattern of advance (year of first detection) of invading populations (bottom): X's = 1994–1997, light gray circles = 1998–1999, and dark gray circles = 2000–2001.

Thus, we combined all native-range occurrences to build a single model for projection to North America.

Projecting our native-range ecological niche model to North America, broad areas were identified as suitable for this species to maintain populations (Fig. 3).

These areas included the entire eastern half of the continent, west as far as the Great Plains. The models also identified disjunct areas of potential distribution along the Pacific Coast; in western, central, and southern Mexico; and in the West Indies. As such, the potential distribution

of *M. sculpturalis* in North America appears to be quite extensive.

DISCUSSION

The potential invaded distribution in North America predicted by our ecological niche model for *M. sculpturalis* considerably exceeds the earlier prediction of Batra (1998). Both predictions agree that the species will come to occupy the humid eastern United States; our model, however, also shows a broader potential to the west and north of the area outlined by Batra (1998). In other words, instead of extending only west to eastern Texas, the species will likely reach northwestern Texas and western Kansas. Similarly, instead of ending in southern New England, the species will likely reach north to Nova Scotia, Canada (Fig. 3).

Projection of our model onto all of North America identified additional potential areas of invaded distribution for the bee *outside* the present eastern range discussed above. These areas are along the Pacific Coast of the United States, portions of Idaho, and parts of Mexico and the West Indies (Fig. 3). These predictions are—it should be remembered—of *potential* distributions only; as such, the species would likely establish populations only if presented with dispersal opportunities that would place them in or close to those areas. Given the potential ecological suitability identified and high import traffic from Asia along the western seaboard there would, however, appear to be a high probability of an independent North American introduction of this species into northern California, and eastern Oregon and Washington. The West Indies also seems to be a credible region into which *M. sculpturalis* might invade. A related species, *M. (Callomegachile) rufipennis* (Fabricius) from Africa, is already adventive in the West Indies (e.g., Mitchell 1980, Genaro 1997), reinforcing the notion that, if introduced, *M. sculpturalis* could easily

become established and widespread on these islands.

The growing number of collection records of the bee in North America so far confirms the predictions presented here. Indeed, plotting known North American occurrences by year (Fig. 3) shows the broadening spatial pattern of occurrence of the species through time. Continued surveying of this species over time will provide much more concrete tests of our predictions, particularly in states such as Kentucky, Illinois, Indiana, Missouri, and Mississippi as well as more western localities in Tennessee. Such surveys will be important for documenting the spread of *M. sculpturalis*. Surveying for *M. sculpturalis* is not difficult, given its impressive size; even indirect records can be accumulated via the marks it leaves on flowers while foraging (Mangum and Sumner 2003). Possible impacts of *M. sculpturalis* on native *Megachile* species, other native bees, or as a pollinator, are entirely unknown. Although it has been seen using abandoned nests of native carpenter bees (Mangum and Sumner 2003), its foraging activities have so far been recorded principally on exotic plants. For the moment there is little reason to *a priori* suspect any barriers to the bee's continued westward invasion of the North American continent.

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