# GIS-BASED CHARACTERIZATION OF THE GEOGRAPHIC DISTRIBUTIONS OF WILD AND CULTIVATED POPULATIONS OF THE MESOAMERICAN FRUIT TREE SPONDIAS PURPUREA (ANACARDIACEAE)[1]

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Humans are having a profound impact on the geographic distributions of plant populations. In crop species, domestication has been accompanied by the geographic expansion of cultivated populations relative to their wild ancestors. We used a geographical information system (GIS)-based approach to investigate differences in the environmental factors characterizing the geographic distributions of cultivated and wild populations of the Mesoamerican fruit tree *Spondias purpurea*. Locality data for 86 cultivated and 28 wild *S. purpurea* populations were used in conjunction with environmental data layers and Maxent, a maximum entropy application for predicting species distributions. Interpredictivity analyses and principal components analysis revealed that the predicted distribution of wild *S. purpurea* is nested within the cultivated distribution and that the ecological niche (defined by environmental characteristics) of cultivated *S. purpurea* has expanded relative to that of wild populations. Significant differences between wild and cultivated populations were detected for five environmental variables, corresponding to the expansion of *S. purpurea* during the domestication process from its native habitat in the Mesoamerican tropical dry forests into less seasonal habitats. These data suggest that humans have altered the range of habitats occupied by cultivated *S. purpurea* populations relative to their wild progenitors.

**Key words:** Anacardiaceae; domestication; Mesoamerica; niche conservatism; species distribution model; *Spondias purpurea*; tropical dry forest.

Humans are influencing the geographic distributions of plants through displacement resulting from habitat destruction, the deliberate spread of economically valuable taxa, and through accidental introductions. In many crop species, the geographic area occupied by cultivated populations has expanded dramatically in recent times relative to the areas occupied by their wild progenitors. This expansion is evidenced by the contemporary distributions of many of the world's most economically important crops (e.g., chilis, cucumbers, oranges, peanuts, pineapples, potatoes, rice, soybeans, tomatoes, wheat), with the bulk of their production on continents other than those where the crop originated (Simpson and Ogorzaly, 1995). Although the expanded geographic distribution of cultivated populations relative to their wild progenitors is well known, specific differences in the environmental characteristics of regions occupied by cultivated vs. wild populations have not been documented. Have humans simply transported cultivated individuals into regions that resemble the habitat of their wild progenitors? Or under human influence, have cultivated populations been able to expand into regions that differ significantly from regions occupied by their wild progenitors?

Plant domestication occurs as humans selectively maintain and/or cultivate in agricultural habitats a subset of wild individuals. During the course of domestication, evolutionary processes such as selection and drift result in morphological and genetic changes in the cultivated populations making them distinct from their wild progenitors (Clegg et al., 1984; Gepts and Clegg, 1989; Ennos, 1997; Eyre-Walker et al., 1998; Saunders et al., 2001; Anthony et al., 2002; Hancock, 2004). Differences in the environmental characteristics of the regions occupied by cultivated and wild populations could reflect human influences (e.g., transportation, watering, fertilization, protection, clearing of competing plants) that facilitate the persistence of cultivated genotypes in regions where, in the absence of the human contributions, the species does not occur. Alternatively, the expanded geographic range of cultivated populations relative to their wild ancestors could be a result of artificial selection for characteristics that allowed populations to inhabit a wider diversity of habitats.

Differences in the environmental characteristics of areas occupied by organisms can be examined by modeling species distributions, a technique that integrates locality data, GIS data, and modeling algorithms (e.g., Anderson et al., 2002; Anderson and Martinez-Meyer, 2004; Elith et al., 2006; Phillips et al., 2006). The resulting distribution model describes the common environmental and climatological characteristics of the known range of a given species or group of populations (Peterson, 2003; Soberón and Peterson, 2004). This approach has been used to predict species distributions (Illoldi-Rangel et al., 2004); to predict the potential geographic range of invading

species (Peterson, 2003; Mau-Crimmins et al., 2006), to examine the evolution of ecological niches (Peterson and Holt, 2003; Rice et al., 2003; Martínez-Meyer et al., 2004a, b; Hoffman, 2005), to investigate speciation mechanisms (Graham et al., 2004), and to predict changes in the distributions of fauna and flora associated with projected models of climate change (Peterson et al., 2002; Siqueira and Peterson, 2003; Oberhauser and Peterson, 2003; Thomas et al., 2004). In crop species, GIS-based analyses have been used to predict yields of different cultivars in various geographic areas (Jeutong et al., 2000; Caldiz et al., 2002), to explore the distributions of wild relatives of crop species (Greene et al., 1999a, b; Hijmans and Spooner, 2001; Jarvis et al., 2004), and to model future distributions of crop pests and diseases (Bernardi, 2001).

In this study, we used GIS data sets and predictive modeling to investigate the environmental and climatological factors characterizing the geographic distributions of cultivated populations and the wild populations from which they were derived. We focused on the Mesoamerican fruit tree *Spondias purpurea* L. (known locally as ciruela Mexicana, jocote, purple mombin, or hog plum), a species cultivated throughout the neotropics and subtropics for its plumlike fruits, which are eaten fresh, sold in local markets, and made into jams and beverages (Avitia García, 1997; Baraona Cockrell, 2000). Although some are intensively cultivated in orchards, the majority of *S. purpurea* trees are planted in informal agricultural habitats such as backyard gardens, living fences, and small multicrop farms (Cuevas, 1994) and have not been subjected to extensive breeding. Cultivated *S. purpurea* trees were derived from wild populations in at least two distinct geographic regions within Mesoamerica (Miller and Schaal, 2005, 2006). Today, the wild (undomesticated) populations of *S. purpurea* can be found in the tropical dry forests of Mexico and Central America (Mandujano et al., 1994; Mooney et al., 1995; Miller and Schaal, 2005, 2006). There are clear morphological differences between cultivated and wild *S. purpurea* populations, indicating that selection and domestication has occurred in this species. Fruits of the wild jocotes are bright red or yellow in some regions (cultivated fruits can be red, orange, yellow, green, or purple) and are smaller and more acidic than the cultivated fruits, with considerably less flesh surrounding the seed. Wild *S. purpurea* trees reproduce from seed and native populations are age-structured with a variety of juvenile and mature individuals present; cultivated *S. purpurea* trees are propagated vegetatively (Miller, 2004).

To quantify differences in the environmental characteristics of regions occupied by cultivated *S. purpurea* populations and wild *S. purpurea* populations, we use field-collected locality data, GIS databases, and the distribution modeling method Maxent to (1) model the predicted area of occurrence of wild *S. purpurea* populations and compare it to the predicted area of occurrence of cultivated *S. purpurea* populations, and (2) characterize the mean and variance of several environmental parameters for wild and cultivated populations of *S. purpurea* and examine the null hypothesis that wild and cultivated populations occur in the same types of habitats.

## MATERIALS AND METHODS

***Sampling***—One hundred and fourteen distinct localities with *S. purpurea* were sampled, and each population included at least one and as many as 80 *S. purpurea* trees. In total, 86 cultivated populations and 28 wild populations from Costa Rica, El Salvador, Guatemala, Honduras, Mexico, Nicaragua, and Panama were included in the study (Table 1, Fig. 1). All populations were visited by the first author (A.J.M.) at least once during field studies that took place in 2000, 2001, 2002, and 2005. Cultivated populations were distinguished from wild populations by (1) habitat: cultivated populations were found in agricultural environments including backyards, living fences, small farms, and orchards; wild populations were found in primary or secondary forests, (2) reproduction: cultivated populations are propagated exclusively vegetatively from large cuttings (the physical form of the tree trunk often reflects this method of propagation); wild populations grow from seeds and have obvious age-structured populations, and (3) fruit morphology: cultivated fruits are much larger and sweeter than wild fruits and have a wide range of colors; wild fruits have very little "meat" (fleshy mesocarp) relative to cultivated fruits they taste very acidic, and are usually red or yellow in color. Herbarium specimens were collected for 105 of the 114 populations and were deposited at the Missouri Botanical Garden (St. Louis, Missouri, USA) and in regional herbaria. Collection numbers 2005-1 through 2005-9 were vouchered digitally and are available upon request from the authors.

***Species distribution modeling***—Locality data for wild and cultivated populations of *S. purpurea* were collected using a Garmin GPS eTrex 010-00190-00 (Garmin International Inc., Olathe, Kansas, USA). Using these locality data (Table 1), Maxent (a method for predicting species distributions; Phillips et al., 2006), and geographic information system (GIS) environmental data layers, we predicted the geographic distribution of wild and cultivated populations of *S. purpurea*. Maxent is a general-purpose machine-learning approach to the modeling of species distributions using presence-only data (Phillips et al., 2006). It predicts the potential distribution of a species by estimating the probability distribution of maximum entropy across a specified region, subject to a set of constraints that represent the missing information (lack of absence data) about the target distribution (Phillips et al., 2006). Like other niche-based models constructed from presence-only data, the predicted distribution describes suitability in ecological (environmental and climatological) space, which is then projected onto geographic space revealing a prediction of the geographic distribution of the taxon of interest (Phillips et al., 2006). For our analyses, we used 18 GIS data layers from the WorldClim Global Climate GIS database (30-s resolution) (Hijmans et al., 2004, 2005). These included topographic and bioclimatic variables representing elevation (m), annual mean temperature (°C), mean diurnal temperature range (°C), isothermality, temperature seasonality (°C), maximum temperature of warmest month (°C), minimum temperature of coldest month (°C), temperature annual range (°C), mean temperature of wettest quarter (°C), mean temperature of driest quarter (°C), mean temperature of warmest quarter (°C), mean temperature of coldest quarter (°C), annual precipitation (mm), precipitation seasonality (mm), precipitation of wettest quarter (mm), precipitation of driest quarter (mm), precipitation of warmest quarter (mm), and precipitation of coldest quarter (mm).

Species distributions were predicted for both wild and cultivated populations using the locality data in Table 1. For each group (wild or cultivated), the Maxent algorithm was run using the default parameters including a maximum of 500 iterations with a convergence threshold of 0.00001. During model development, 50% of the localities were used for model training, while 50% of the localities were held back to test model accuracy. Cumulative probability distributions ranging from 0 to 100 were generated for both wild and cultivated populations that represent a relative measure of the probability of occurrence for the modeled group. A binomial probability distribution was applied to the localities that were held back for model testing to assess the accuracy of each predicted distribution (Phillips et al., 2006).

To assess the interpredictivity of the cultivated and wild model predictions, we used a binomial probability distribution to determine whether the number of times that the occurrence data points from wild populations overlapped a threshold-based predicted distribution of cultivated populations was different than random and vice versa (Peterson et al., 1999; Rice et al., 2003; Knouft et al., 2006). The distribution threshold was set at the minimum probability area containing all of the training localities (Phillips et al., 2006). Although Maxent produces a modeled species distribution with relative probabilities of occurrence between 0 and 100, the minimum probability threshold allows for identification of a standardized percentage of the distribution area, thus allowing for comparisons of different models (e.g., wild and cultivated) (Phillips et al., 2006). The interpredictivity analysis tests whether the percentage of actual occurrence data points for cultivated populations that falls within the modeled distribution of the wild populations corresponds to the proportion of land area in Mexico and Central America that is covered by the

Fig. 1.   Localities of cultivated (gray circles) and wild (black triangles) *S. purpurea* populations used in this study.

wild *S. purpurea* predicted distribution. Greater than expected overlap is consistent with the idea that domestication has not been accompanied by a significant shift or expansion in the ecological factors characterizing the distribution of cultivated *S. purpurea* populations; alternatively, less than expected overlap or overlap that does not deviate from a random frequency may indicate that the distribution of cultivated *S. purpurea* populations has shifted and/or expanded relative to the distribution of the wild ancestors.

As an additional test of the reciprocal quality of each prediction, the interpredictive effectiveness of each model was directly compared. For this analysis, values from the cumulative probability distribution for cultivated populations were extracted at actual wild localities. Similarly, values from the cumulative probability distribution for wild populations were extracted at actual cultivated localities. The extracted values were compared using a Mann–Whitney *U* test.

In addition to investigating distribution similarity using species locality data and the predictions generated by the Maxent algorithms, we qualitatively examined the overlap of the "environmental envelopes" of wild and cultivated populations using GIS-derived topographic and environmental data extracted from localities for each group (wild and cultivated). We generated the environmental envelope for each group based on data extracted from the 18 WorldClim Global Climate GIS variables used in the Maxent analyses (30-s resolution) (Hijmans et al., 2004, 2005). Environmental data for each group were compiled by importing population locality points (Table 1) into DIVA-GIS (Hijmans et al., 2001). Environmental data were then extracted from each GIS layer to provide 18 topographic and climatic measures for each locality point. All topographic and climatic data were $\log_{10}$-transformed to standardize data for statistical analyses. A principal components analysis (PCA) was performed on the correlation matrix of transformed data to generate data needed to construct an environmental envelope based on information from the wild as well as the cultivated data sets. To generate and compare the environmental envelope of each group, principal component scores from the first three axes of the PCA were plotted in *x*, *y* space for the wild and cultivated populations (similar to Knouft et al., 2006).

***Comparisons of wild and cultivated population environmental variables***—Using DIVA-GIS we compiled topographic and environmental data for wild and cultivated populations from GIS data sets based on the localities in Table 1. To avoid redundancy among variables (e.g., mean temperature warmest quarter, mean temperature warmest month), we selected 10 layers (Tables 2, 3) from the 30-s resolution 30-yr WorldClim data sets (Hijmans et al., 2004) to use in the comparison. Each topographic and environmental measure for wild and cultivated populations was compared using a Mann–Whitney *U* test. The variances of environmental variables were compared between wild and cultivated populations by calculating an *F* statistic to determine if these two groups occurred in regions with differing ranges of environmental characteristics. Because multiple tests were performed for each set of analyses, we applied a sequential Bonferroni correction to our tests ($\alpha = 0.05$) (Holm, 1979).

Because we had approximately three times more cultivated localities than wild localities, we conducted a final set of analyses to examine the influence of sample size on our assessments of differences between means and variances of environmental variables for the wild and cultivated datasets. A 95% confidence interval was generated for cultivated topographic and environmental variables by randomly resampling 28 values (the number of wild localities) from each cultivated topographic and environmental data set. The mean and variance of these 28 values was calculated, and this process was repeated 1000 times. The 95% confidence intervals generated from these resampling iterations were compared to the relevant mean and variance from the wild populations to assess whether significant differences detected in the previous Mann–Whitney analyses were due to varying sample sizes between the wild and cultivated datasets.

## RESULTS

***Species distribution modeling***—Based on known occurrences of cultivated *S. purpurea* populations and their wild progenitors, we generated distribution maps predicting the possible areas where cultivated and wild *S. purpurea* populations might occur (Fig. 2a, b). Predictions for both wild and cultivated populations were highly significant based on a binomial probability distribution test calculated from the held-back test localities (Wild AUC of ROC: training data = 0.975, test data = 0.914, *P* < 0.0001; Cultivated AUC of ROC: training data = 0.929, test data = 0.889, *P* < 0.0001).

The threshold-based interpredictivity analyses indicate that the cultivated predicted distribution encompasses a significantly greater number of wild localities than expected by chance (28 of 28, *P* < 0.0001). The predicted distribution of wild populations, however, does not encompass a significantly greater number of cultivated localities than expected by chance (29 of 86, *P* = 0.2092). Direct comparison of reciprocal predictive abilities of both models suggests that the cultivated predicted distribution provides a higher degree of accuracy for the actual wild localities than the wild prediction does for the cultivated localities ($U_{\text{stat}} = 2086.0$, *P* < 0.0001).

The first three principal components explained 81.36% of the overall variance in the data (PC1 = 38.14%, PC2 = 29.08%, PC3 = 14.14%; Appendix 1). Comparisons of the principal component scores between wild and cultivated populations in two-dimensional space indicates that the environmental envelope of wild populations is nested within the environmental envelope of cultivated populations in all cases (Fig. 3).

***Comparisons of wild and cultivated population environmental variables***—Significant differences between wild and cultivated populations were detected for five environmental variables: mean diurnal temperature range, annual temperature range, annual precipitation, precipitation seasonality, and precipitation in the driest quarter (Table 2). The values for mean diurnal temperature range, annual temperature range, and precipitation seasonality were significantly greater for wild populations as compared with cultivated populations. The values for annual precipitation and precipitation in the driest month and in the driest quarter were significantly greater for cultivated populations as compared to wild populations. Cultivated populations had significantly greater variances than wild populations for five environmental variables: mean diurnal temperature range, annual temperature range, annual precipitation, precipitation seasonality, and precipitation in the driest quarter (Table 3). Results from the generation of confidence intervals suggest that sample size differences between the wild and cultivated data sets are not influencing the results from these comparisons (Tables 2, 3).

TABLE 1. Localities of cultivated and wild *S. purpurea* populations. Voucher specimens were deposited at MO and in herbaria in the country of origin.

| Cultivated/Wild | Latitude | Longitude | Elev (m) | Country | Province/State | Collection no. |
|---|---|---|---|---|---|---|
| Cultivated | 09°57′06.0″N | 84°28′29.8″W | 627 | Costa Rica | Alajuela | AM 222, 223 |
| Cultivated | 10°08′16.3″N | 85°25′13.7″W | 123 | Costa Rica | Guanacaste | AM 204 |
| Cultivated | 10°28′50.2″N | 85°36′15.5″W | 49 | Costa Rica | Guanacaste | AM 205, 206 |
| Cultivated | 09°58′41.9″N | 84°45′15.9″W | 12 | Costa Rica | Puntarenas | AM 202 |
| Cultivated | 09°15′39.6″N | 83°51′48″W | 31 | Costa Rica | Puntarenas | AM 211 |
| Cultivated | 08°28′10.3″N | 83°17′03.1″W | 35 | Costa Rica | Puntarenas | AM 215 |
| Cultivated | 08°26′25.4″N | 83°25′48.9″W | 25 | Costa Rica | Puntarenas | AM 219 |
| Cultivated | 09°53′06.0″N | 84°27′23.2″W | 397 | Costa Rica | San Jose | AM 224 |
| Cultivated | 13°50′52.1″N | 90°00′31.3″W | 315 | El Salvador | Ahuachapán | AM 141–144 |
| Cultivated | 13°54′13.3″N | 88°58′23″W | 320 | El Salvador | Cabañas | AM 137 |
| Cultivated | 13°43′22.1″N | 89°39′43.2″W | 358 | El Salvador | Sonsonate | AM 146 |
| Cultivated | 13°44′35″N | 89°39′28.7″W | 417 | El Salvador | Sonsonate | AM 147 |
| Cultivated | 15°24′14″N | 89°38′19.6″W | 19 | Guatemala | Altaverapaz | AM 129 |
| Cultivated | 14°56′11.2″N | 90°12′6.7″W | 911 | Guatemala | El Progresso | AM 131 |
| Cultivated | 14°21′24.5″N | 90°32′19.9″W | 1378 | Guatemala | Guatemala | AM 109 |
| Cultivated | 14°30′26.3″N | 90°31′09.8″W | 1697 | Guatemala | Guatemala | AM 110 |
| Cultivated | 14°27′17.5″N | 90°34′17.9″W | 1268 | Guatemala | Guatemala | AM 112 |
| Cultivated | 15°16′12.7″N | 89°04′42.1″W | 111 | Guatemala | Izabol | AM 121 |
| Cultivated | 15°40′46.1″N | 88°38′06.6″W | 26 | Guatemala | Izabol | AM 123 |
| Cultivated | 15°37′34.6″N | 89°03′26.4″W | 28 | Guatemala | Izabol | AM 126 |
| Cultivated | 15°31′35.2″N | 89°20′32.5″W | 13 | Guatemala | Izabol | AM 127 |
| Cultivated | 14°43′43.7″N | 91°15′47.7″W | 1588 | Guatemala | Solala | AM 114–118 |
| Cultivated | 15°01′02.2″N | 89°40′45.1″W | 257 | Guatemala | Zacapa | AM 119 |
| Cultivated | 13°14′29.0″N | 87°09′42.8″W | 58 | Honduras | Choluteca | AM 171 |
| Cultivated | 13°16′09.1″N | 87°08′11.6″W | 360 | Honduras | Choluteca | AM 172 |
| Cultivated | 13°15′35″N | 87°07′58″W | 568 | Honduras | Choluteca | AM 176 |
| Cultivated | 13°41′21.8″N | 87°19′48.5″W | 160 | Honduras | Choluteca | AM 167, 168 |
| Cultivated | 14°32′03.5″N | 87°48′01.1″W | 1249 | Honduras | Comayagua | AM 155 |
| Cultivated | 13°59′47.9″N | 87°02′10.4″W | 878 | Honduras | Fco. Morazon | AM 166 |
| Cultivated | 13°58′10.92″N | 86°59′38.2″W | 789 | Honduras | Fco. Morazon | AM 149A |
| Cultivated | 14°22′22.9″N | 87°39′26″W | 589 | Honduras | La Paz | AM 150C |
| Cultivated | 14°22′02.3″N | 87°39′13.1″W | 593 | Honduras | La Paz | AM 152, 153 |
| Cultivated | 14°36′48.4″N | 86°14′28.1″W | 383 | Honduras | Olancho | AM 161 |
| Cultivated | 14°37′13.6″N | 86°25′54.4″W | 645 | Honduras | Olancho | AM 162 |
| Cultivated | 16°46′05.4″N | 93°22′55.2″W | 805 | Mexico | Chiapas | AM 324 |
| Cultivated | 16°31′40.8″N | 92°49′46.5″W | 456 | Mexico | Chiapas | AM 327 |
| Cultivated | 16°44′44.6″N | 93°30′34.3″W | 709 | Mexico | Chiapas | AM 328 |
| Cultivated | 19°01′12.4″N | 104°07′11.5″W | 31 | Mexico | Colima | AM 295 |
| Cultivated | 16°48′29.4″N | 99°21′45.9″W | 115 | Mexico | Guerrero | AM 336 |
| Cultivated | 20°50′16.4″N | 103°19′36.8″W | 934 | Mexico | Jalisco | AM 275–276 |
| Cultivated | 20°51′37.0″N | 103°20′22.9″W | 1086 | Mexico | Jalisco | AM 277, 278 |
| Cultivated | 20°06′36.9″N | 105°18′39.0″W | 95 | Mexico | Jalisco | AM 289 |
| Cultivated | 19°13′34.1″N | 104°38′23.8″W | 15 | Mexico | Jalisco | AM 294 |
| Cultivated | 19°27′26.9″N | 103°49′24.7″W | 709 | Mexico | Jalisco | AM 298 |
| Cultivated | 20°51′34.6″N | 103°20′23.5″W | 1082 | Mexico | Jalisco | AM 2005-2 |
| Cultivated | 20°16′50.7″N | 105°23′46.3″W | 1545 | Mexico | Jalisco | AM 2005-9 |
| Cultivated | 20°50′14.4″N | 103°19′37.0″W | 935 | Mexico | Jalisco | AM 2005-1 |
| Cultivated | 18°29′59.8″N | 103°29′06.8″W | 99 | Mexico | Michoacan | AM 301 |
| Cultivated | 19°04′06.4″N | 102°26′57.6″W | 244 | Mexico | Michoacan | AM 304 |
| Cultivated | 19°00′30.9″N | 102°20′16.0″W | 257 | Mexico | Michoacan | AM 306 |
| Cultivated | 19°20′58.4″N | 101°55′03.7″W | 1209 | Mexico | Michoacan | AM 307, 308 |
| Cultivated | 21°33′27.9″N | 104°56′17.1″W | 812 | Mexico | Nayarit | AM 280 |
| Cultivated | 21°35′38.7″N | 104°59′57.0″W | 578 | Mexico | Nayarit | AM 281 |
| Cultivated | 21°38′47.9″N | 105°07′27.2″W | 64 | Mexico | Nayarit | AM 283 |
| Cultivated | 21°37′01.5″N | 104°58′03.3″W | 632 | Mexico | Nayarit | AM 2005-4 |
| Cultivated | 21°33′28.7″N | 104°56′17.6″W | 825 | Mexico | Nayarit | AM 2005-3 |
| Cultivated | 16°42′52.0″N | 94°44′53.1″W | 125 | Mexico | Oaxaca | AM 319 |
| Cultivated | 16°11′34.8″N | 95°04′22.1″W | 8 | Mexico | Oaxaca | AM 330 |
| Cultivated | 15°55′37.0″N | 95°56′01.7″W | 202 | Mexico | Oaxaca | AM 331 |
| Cultivated | 15°49′49.2″N | 96°20′16.1″W | 256 | Mexico | Oaxaca | AM 332 |
| Cultivated | 16°01′21.1″N | 97°04′02.0″W | 598 | Mexico | Oaxaca | AM 334 |
| Cultivated | 18°37′41.1″N | 96°24′56.2″W | 93 | Mexico | Veracruz | AM 310 |
| Cultivated | 17°52′37.4″N | 96°12′03.7″W | 684 | Mexico | Veracruz | AM 314 |
| Cultivated | 18°14′20.0″N | 94°52′25.1″W | 472 | Mexico | Veracruz | AM 315 |
| Cultivated | 18°09′16.2″N | 94°47′28.3″W | 65 | Mexico | Veracruz | AM 316 |
| Cultivated | 18°04′45.5″N | 94°42′11.7″W | 30 | Mexico | Veracruz | AM 317 |
| Cultivated | 20°23′16.0″N | 89°25′0.97″W | 20 | Mexico | Yucatan | AM 260 |
| Cultivated | 20°23′06.1″N | 89°23′45.9″W | 20 | Mexico | Yucatan | AM 261–263 |
| Cultivated | 20°52′31.1″N | 89°15′56.6″W | 13 | Mexico | Yucatan | AM 264 |

TABLE 1.    Continued.

| Cultivated/Wild | Latitude | Longitude | Elev (m) | Country | Province/State | Collecton no. |
|---|---|---|---|---|---|---|
| Cultivated | 20°49′08.8″N | 89°14′46.9″W | 20 | Mexico | Yucatan | AM 265–268 |
| Cultivated | 12°26′36.3″N | 85°36′19.9″W | 419 | Nicaragua | Boaco | AM 187 |
| Cultivated | 11°57′54.9″N | 86°30′39.0″W | 120 | Nicaragua | Managua | AM 199, 200 |
| Cultivated | 11°59′45.2″N | 86°07′21.6″W | 175 | Nicaragua | Masaya | AM 178 |
| Cultivated | 12°58′02.9″N | 85°58′32.1″W | 858 | Nicaragua | Matagalpa | AM 198 |
| Cultivated | 13°44′38.3″N | 86°06′35.2″W | 675 | Nicaragua | Nueva Segovia | AM 195 |
| Cultivated | 08°54′52.4″N | 82°11′10.4″W | 90 | Panama | Bocas del Toro | AM 258 |
| Cultivated | 08°15′45.6″N | 82°52′04.4″W | 55 | Panama | Chiriqui | AM 260 |
| Cultivated | 08°10′43.1″N | 82°52′35.8″W | 35 | Panama | Chiriqui | AM 262, 263 |
| Cultivated | 07°44′50.9″N | 80°14′17.4″W | 63 | Panama | Los Santos | AM 245 |
| Cultivated | 07°44′35.7″N | 80°15′48.3″W | 91 | Panama | Los Santos | AM 241, 243 |
| Cultivated | 07°27′06.7″N | 80°31′04.9″W | 56 | Panama | Los Santos | AM 248–250 |
| Cultivated | 09°13′09.9″N | 78°57′54.3″W | 32 | Panama | Panama | AM 233 |
| Cultivated | 09°13′13.2″N | 78°55′03.6″W | 32 | Panama | Panama | AM 236 |
| Cultivated | 08°33′40.9″N | 79°57′02.2″W | 124 | Panama | Panama | AM 237, 238 |
| Cultivated | 08°29′59.8″N | 81°04′13.9″W | 290 | Panama | Veraguas | AM 254 |
| Cultivated | 08°30′39.2″N | 81°04′52.4″W | 288 | Panama | Veraguas | AM 255 |
| Wild | 10°48′14.3″N | 85°38′25.9″W | 200 | Costa Rica | Guanacaste | AM 208, 209 |
| Wild | 13°53′13.1″N | 88°57′43″W | 374 | El Salvador | Cabañas | AM 133, 136 |
| Wild | 14°25′59″N | 90°38′40.3″W | 1278 | Guatemala | Guatemala | AM 111 |
| Wild | 16°42′19.8″N | 93°31′55.7″W | 652 | Mexico | Chiapas | AM 323 |
| Wild | 16°54′47.2″N | 93°06′10.6″W | 706 | Mexico | Chiapas | AM 325 |
| Wild | 16°45′16.4″N | 92°58′18.3″W | 679 | Mexico | Chiapas | AM 326 |
| Wild | 19°01′12.4″N | 104°07′11.5″W | 31 | Mexico | Colima | AM 297 |
| Wild | 16°48′2.4″N | 99°21′25.2″W | 120 | Mexico | Guerrero | AM 337 |
| Wild | 20°33′38.1″N | 105°15′20.2″W | 15 | Mexico | Jalisco | AM 287 |
| Wild | 20°15′26.7″N | 105°18′55.6″W | 416 | Mexico | Jalisco | AM 288 |
| Wild | 19°38′23.2″N | 105°10′04.7″W | 39 | Mexico | Jalisco | AM 290 |
| Wild | 19°17′53.1″N | 104°46′54.3″W | 28 | Mexico | Jalisco | AM 291 |
| Wild | 19°29′53.2″N | 105°02′40.2″W | 105 | Mexico | Jalisco | AM 293 |
| Wild | 19°35′09.8″N | 104°00′56.3″W | 720 | Mexico | Jalisco | AM 299 |
| Wild | 20°15′18.1″N | 105°18′50.0″W | 398 | Mexico | Jalisco | AM 2005-7 |
| Wild | 20°07′31.7″N | 105°18′55.9″W | 128 | Mexico | Jalisco | AM 2005-8 |
| Wild | 18°29′59.8″N | 103°29′06.8″W | 99 | Mexico | Michoacan | AM 300 |
| Wild | 18°20′23.7″N | 102°17′20.5″W | 821 | Mexico | Michoacan | AM 302 |
| Wild | 18°23′15.7″N | 102°10′44.9″W | 604 | Mexico | Michoacan | AM 303 |
| Wild | 19°04′06.4″N | 102°26′57.6″W | 244 | Mexico | Michoacan | AM 305 |
| Wild | 21°37′01.5″N | 104°58′03.3″W | 632 | Mexico | Nayarit | AM 279 |
| Wild | 21°41′32.5″N | 105°04′06.5″W | 182 | Mexico | Nayarit | AM 282 |
| Wild | 21°19′41.3″N | 105°11′04.5″W | 38 | Mexico | Nayarit | AM 286 |
| Wild | 21°19′44.3″N | 105°11′01.4″W | 11 | Mexico | Nayarit | AM 2005-5 |
| Wild | 16°22′54.6″N | 95°19′05.8″W | 337 | Mexico | Oaxaca | AM 329 |
| Wild | 12°26′32″N | 85°40′55.4″W | 295 | Nicaragua | Boaco | AM 183, 184 |
| Wild | 13°14′59.6″N | 86°21′28.2″W | 823 | Nicaragua | Esteli | AM 197 |
| Wild | 12°23′07.5″N | 86°05′47.5″W | 56 | Nicaragua | Managaua | AM 182 |

## DISCUSSION

During the domestication of *S. purpurea*, humans preferentially cultivated trees with an abundance of large, juicy, sweet fruits resulting in increased variation in the color, size, and taste of *S. purpurea* fruits in cultivated populations (Miller, 2004). Further, domestication of *S. purpurea* resulted in reduced levels of genetic variation in cultivated *S. purpurea* populations as compared with their wild progenitors (Miller and Schaal, 2006). Here, we have identified another fundamental difference between wild and cultivated *S. purpurea* populations. Cultivated populations occupy an expanded geographic distribution relative to their wild progenitors, and there are measurable differences in the environmental factors that characterize the distributions of cultivated and wild *S. purpurea* populations.

***Species distribution models and the evolution of the "ecological niche" in a domesticated species***—Species distribution models based on environmental and climatological factors have been referred to as a representation of the "ecological niche" of a species, or the range of biotic and abiotic characteristics in which a species is able to persist (Peterson, 2003 and references therein; Martínez-Meyer et al., 2004a); however, there is debate in the literature about what exactly the modeled ecological niche represents. Some authors assume that the ecological niche model represents the fundamental ecological niche, which is the range of all theoretical possibilities where a given species could live, defined in coarse-scale climatic dimensions (the "bioclimatic envelope" or the "climatic niche") (Pearson and Dawson, 2003; Soberón and Peterson, 2005). The assumption is that by examining species across their entire geographic distributions, a view of the fundamental ecological niche can be assembled
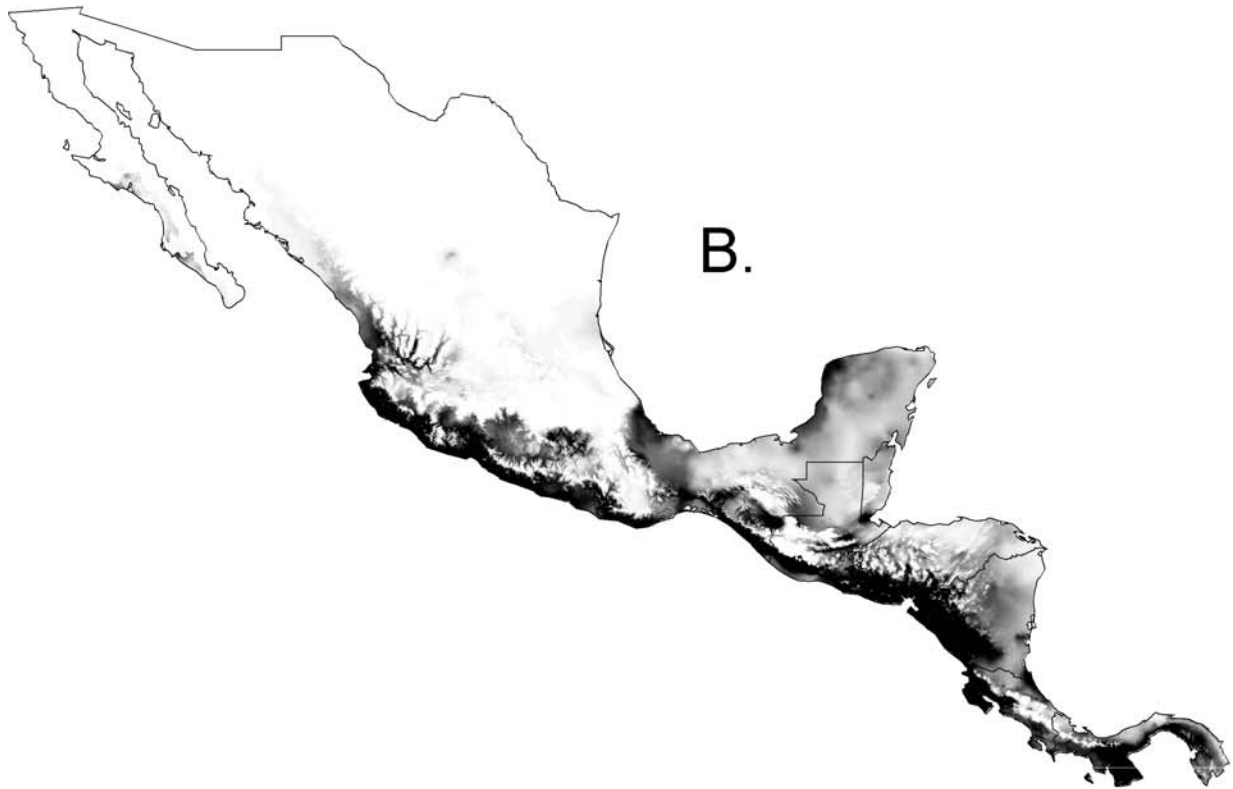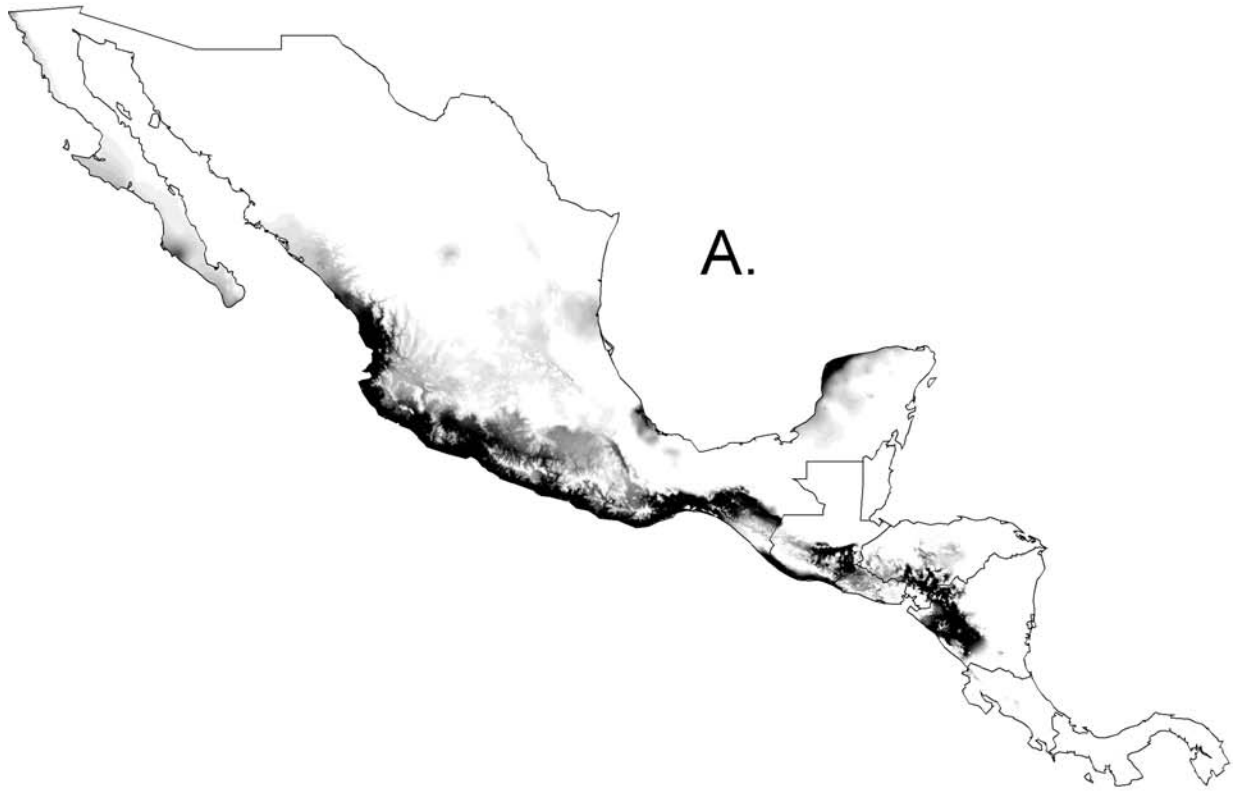
TABLE 2.  Results of comparisons between environmental variables for wild (N = 28) and cultivated (N = 86) populations extracted from GIS layers using a Mann–Whitney U test. One asterisk (*) indicates significance after applying a sequential Bonferroni correction (10 tests) to the results when α = 0.05. Two asterisks (**) indicate that results from the Mann–Whitney U test are supported by confidence intervals (CI) generated from simulations accounting for sample size differences between wild and cultivated population data sets.

| Environmental variable | U | Wild mean ($\sigma$) | Cultivated mean ($\sigma$) | P | 95% CI |
|---|---|---|---|---|---|
| Elevation (m) | 1217.0 | 373.9 (369.35) | 405.6 (408.23) | 0.936 | 284.3–531.3 |
| Mean annual temperature (°C) | 1225.0 | 25.0 (1.88) | 24.9 (2.11) | 0.896 | 24.2–25.6 |
| Mean diurnal temperature range (°C) | 1608.0 | 12.6 (1.42) | 11.6 (2.28) | 0.007* | 11.0–12.4** |
| Annual temperature range (°C) | 1642.5 | 17.9 (2.34) | 16.4 (3.78) | 0.003* | 15.3–17.6** |
| Mean temperature warmest quarter (°C) | 1361.5 | 26.9 (2.09) | 26.5 (2.11) | 0.300 | 25.9–27.1 |
| Mean temperature coldest quarter (°C) | 1352.0 | 22.9 (1.98) | 23.2 (2.49) | 0.334 | 22.4–24.0 |
| Annual precipitation (mm) | 1665.0 | 1161.0 (357.37) | 1642.2 (789.88) | 0.002* | 1404.9–1887.8** |
| Precipitation seasonality (mm) | 1851.5 | 111.6 (13.30) | 90.8 (22.22) | <0.001* | 83.5–97.8** |
| Precipitation wettest quarter (mm) | 1387.0 | 749.7 (261.80) | 837.3 (321.65) | 0.231 | 744.8–940.4 |
| Precipitation driest quarter (mm) | 1762.5 | 15.1 (8.41) | 61.3 (81.81) | <0.001* | 36.6–89.1** |

(Peterson et al., 1999; Peterson, 2001; Wiens and Graham, 2005). Others, however, have suggested that the ecological niche, which is modeled from known localities, represents an approximation of the species' realized niche, the subset of the fundamental niche that it actually occupies in the study area and environmental dimensions being considered (Phillips et al., 2006). In this study, distribution models were produced based on known localities of extant *S. purpurea* populations in Mesoamerica; therefore, in this discussion we assume that the distribution models produced for cultivated and wild *S. purpurea* populations approximate the realized ecological niches of the two groups examined in this region.

The constancy of ecological niches within evolutionary lineages is an important topic in evolutionary ecology: the use of ecological niche models to predict unsampled localities, areas of potential range expansion, and future distributions based on global climate change models depends fundamentally upon the assumption that niches are relatively stable over time (e.g., Peterson et al., 1999; Peterson, 2001, 2003; Peterson and Holt, 2003; Illoldi-Rangel et al., 2004, Mau-Crimmins et al., 2006). Results from a variety of taxa provide evidence for phylogenetic niche conservation (the tendency of species to retain similar ecological niches over evolutionary time scales) at the interspecific level and above (Peterson et al., 1999; Martínez-Meyer et al., 2004a, b; Wiens, 2004). Studies of intraspecific changes in the ecological niche, however, are relatively rare, with previous investigations focusing on insular passerine birds (Scott et al., 2003), monarch butterflies (Oberhauser and Peterson, 2003), diurnal raptors (Galeotti and Rubolini, 2004), and Mexican birds (Peterson and Holt, 2003). Domesticated species present an excellent opportunity

to investigate intraspecific niche differentiation under intense artificial selection that takes place on a relatively short time scale (<10 000 years), facilitating an understanding of some potential impacts of humans on species distributions.

Distribution models constructed here indicate that the ecological niche of *S. purpurea* populations has been conserved during the evolution of the *S. purpurea* lineage. Interpredictivity analyses reveal that 100% of the actual sampled localities of the wild ancestors are contained within the predicted distribution of the cultivated *S. purpurea* populations. Of broader relevance to crop biologists is our finding that the predicted geographic distribution of the wild *S. purpurea* populations is not a good indicator of sites of cultivated *S. purpurea* populations (the predicted distribution of the wild *S. purpurea* populations encompassed just 34% of actual sampled localities of cultivated *S. purpurea*). Rather, it is the predicted distribution of cultivated *S. purpurea* populations that functions as a good indicator of the locations of wild populations. PCA analyses provide further support for conservation of the niche of wild populations within the niche of the cultivated populations: the portion of the PCA space occupied by wild localities is contained within the portion of PCA space occupied by the cultivated populations (Fig. 3). During the domestication of *S. purpurea*, the ecological and environmental characteristics of the regions occupied by wild populations have been retained and represent a subset of the regions occupied by cultivated populations.

In addition, data presented here indicate that the niche of cultivated *S. purpurea* has expanded significantly relative to the niche of the wild populations during the course of domestication. Approximately 66% of the cultivated popula-

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Fig. 2.   Predicted distributions of (A) wild and (B) cultivated *Spondias purpurea* in Mesoamerica based on results of Maxent species distribution models. Distributions are presented as the cumulative relative probabilities of species presence. Lighter areas represent regions with lower relative probabilities of occurrence while darker areas represent regions with higher relative probabilities of occurrence.
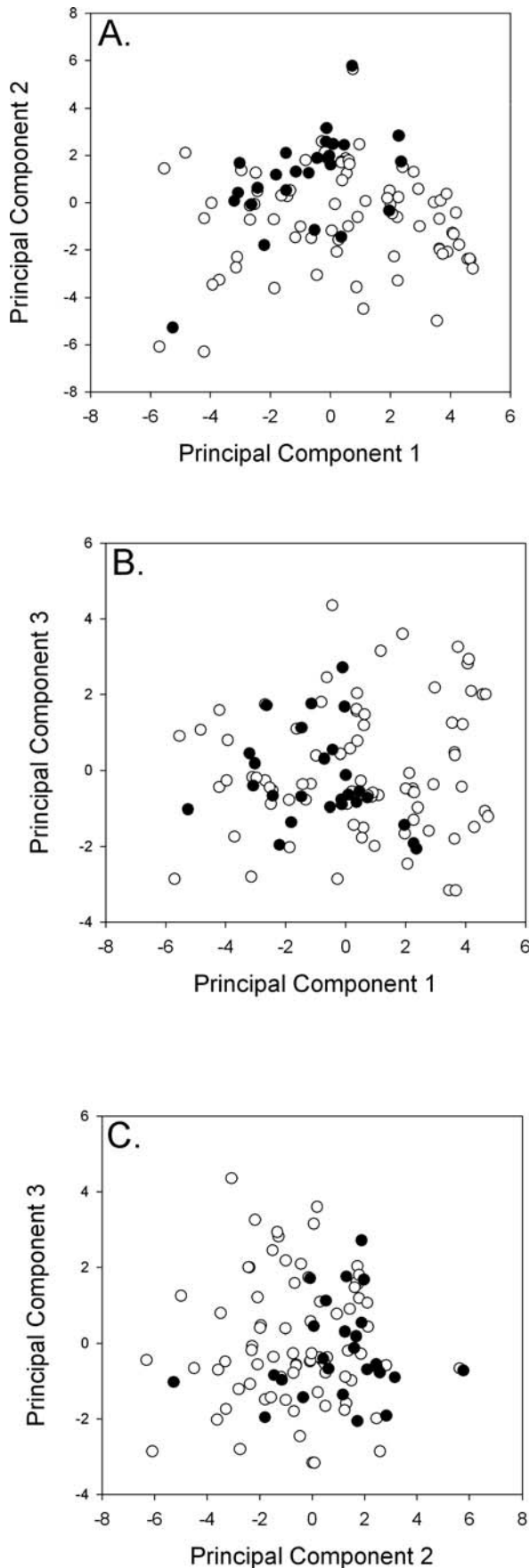
tions fall outside of the predicted distribution of wild *S. purpurea* populations. Further, in the PCA analyses the cultivated populations occupy a much broader portion of the PCA space than the wild populations (Fig. 3). Finally, cultivated populations have significantly higher variances in five environmental variables (Table 3). Humans have facilitated the expansion of cultivated *S. purpurea* populations into regions where, in nature, wild *S. purpurea* populations are not found.

***The impact of cultivation on specific aspects of habitat occupied by S. purpurea***—In addition to providing evidence for differences in the geographic distributions of cultivated and wild *S. purpurea* populations, our data reveal that cultivated and wild *S. purpurea* populations do not occur in exactly the same varieties of habitats. We have identified specific climatological factors that differ in mean and variance between cultivated and wild populations (Table 2). The geographic regions occupied by cultivated populations are wetter throughout the year and less seasonal than the geographic regions occupied by wild *S. purpurea* populations. Wild *S. purpurea* populations are found in the Mesoamerican dry forests, which have a wide temperature range and marked seasonality characterized by distinct wet and dry seasons (Murphy and Lugo, 1986). Cultivated populations are found in these areas as well as regions with less pronounced seasonality and more rainfall. In previous studies, researchers have documented vegetation changes in the tropical dry forests following intensive anthropogenic disturbances (Burgos and Maas, 2004) and have tracked succession history following agriculture and grazing on lands previously occupied by tropical dry forests (Ruiz et al., 2005). There are, however, no known studies documenting the expansion of a dry forest species into other habitats. In the case of *S. purpurea*, selection during the domestication process produced a measurable change in habitat in this dry forest native.

Differences in the environmental and climatological factors characterizing the geographic distributions of cultivated and wild populations could be the result of selection during the domestication process for trees that can survive in a wide variety of habitats. The relatively expanded geographic distribution of cultivated populations could reflect the various contributions of humans toward the survival of trees in agricultural habitats, including the facilitation of transport and reproduction, elimination of competition, and supply of water and additional resources. Alternatively, the relatively limited distribution of wild *S. purpurea* populations in nature could be the product of competition and prehuman biogeographical history. One of the reasons *S. purpurea* was chosen for this study is that the majority of cultivated *S. purpurea* populations have yet to undergo the intensive selection, breeding, and care associated with modern agriculture. None

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Fig. 3. Results of the principal components analysis performed on the correlation matrix of transformed environmental data for cultivated and wild populations of *S. purpurea*. The first three principal components explained 81.36% of the overall variance (PC1 = 38.14%, PC2 = 29.08%, PC3 = 14.14%). (A) Plot of principal component 1 and 2 scores, (B) plot of principal component 1 and 3 scores, and (C) plot of principal component 2 and 3 scores. Black circles represent scores from wild populations, while white circles represent scores from cultivated populations.

TABLE 3.   Comparisons of the variances of environmental measures of wild populations ($N = 28$) to variances from cultivated populations ($N = 86$). One asterisk (*) indicates significance after applying a sequential Bonferroni correction (10 tests) to the results when $\alpha = 0.05$. Two asterisks (**) indicate that results from the Mann–Whitney $U$-test are supported by confidence intervals generated from simulations accounting for sample size differences between wild and cultivated population datasets.

| Environmental variable | Wild variance | Cultivated variance | $F_{85, 27}$ | $P$ | 95% CI |
|---|---|---|---|---|---|
| Elevation (m) | 136 420.65 | 166 653.56 | 1.221 | 0.284 | 96 586.0–242 390.0 |
| Mean annual temperature (°C) | 3.53 | 4.44 | 1.260 | 0.252 | 2.70–6.41 |
| Mean diurnal temperature range (°C) | 2.02 | 5.22 | 2.590 | 0.003* | 2.89–7.78** |
| Annual temperature range (°C) | 5.47 | 14.30 | 2.615 | 0.003* | 6.77–22.19** |
| Mean temperature warmest quarter (°C) | 4.38 | 4.44 | 1.014 | 0.504 | 2.11–6.98 |
| Mean temperature coldest quarter (°C) | 3.93 | 6.18 | 1.572 | 0.092 | 4.09–8.23 |
| Annual precipitation (mm) | 127 715.56 | 623 911.83 | 4.885 | <0.001* | 295 820.0–975880.0** |
| Precipitation seasonality (mm) | 176.81 | 493.51 | 2.791 | 0.002* | 338.87–657.67** |
| Precipitation wettest quarter (mm) | 68 538.45 | 103 463.92 | 1.510 | 0.113 | 55 368.0–161 100.0 |
| Precipitation driest quarter (mm) | 70.69 | 6692.99 | 94.678 | <0.001* | 1514.4–12648.0** |

of the cultivated populations included in this study were fertilized, watered, or protected to increase the ability of individual trees to survive in a particular region. The only form of deliberate care we observed was the clearing of debris from underneath some cultivated trees. Therefore, it is our interpretation that differences observed in the environmental and climatological characteristics of *S. purpurea* populations reflect real differences in their distributions. These data set up the testable hypothesis that these differences reflect artificial selection during domestication; however, reciprocal transplant experiments are required to determine if there is a heritable basis for the habitat differences.

***Implications of ecological and climatological data for cultivation and conservation of S. purpurea***—*Spondias purpurea* produces juicy, plumlike fruits that are high in vitamin C; it has been identified as a very promising tree crop because it is highly drought-resistant and it grows on poor soil (Cuevas, 1994). Our data corroborate observations that cultivated *S. purpurea* populations can (and do) grow in a wide range of habitats, highlighting its importance as a regional cash crop.

In addition, these data reveal that the distribution of wild *S. purpurea* populations is remarkably narrow relative to the cultivated descendents. The native habitat of the wild progenitors of cultivated *S. purpurea*, the Mesoamerican dry forests, is characterized by several months of severe drought (Mooney et al., 1995; Trejo and Dirzo, 2002); the floristic composition includes primarily small deciduous trees, lianas, and shrubs (Trejo and Dirzo, 2002). It has been estimated that less than 2% of the tropical dry forests remain (Janzen, 1988). The results of this study emphasize the uniqueness of wild *S. purpurea* populations and the habitats in which they evolved, and underscore the importance of their conservation.

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APPENDIX 1.   Principal component 1 (PC1), PC2, and PC3 loadings from principal components analysis of topographic and environmental variables for wild and cultivated populations of *Spondias purpurea*.

| Environmental variable | PC1 | PC2 | PC3 |
|---|---|---|---|
| Elevation | −0.757 | −0.257 | −0.175 |
| Mean annual temperature | 0.798 | 0.597 | −0.002 |
| Mean diurnal temperature | −0.636 | 0.556 | 0.049 |
| Isothermality | 0.301 | −0.187 | −0.814 |
| Temperature seasonality | −0.454 | 0.474 | 0.681 |
| Maximum temperature warmest month | 0.316 | 0.830 | 0.236 |
| Minimum temperature coldest month | 0.926 | 0.023 | −0.238 |
| Temperature annual range | −0.671 | 0.557 | 0.356 |
| Mean temperature wettest quarter | 0.564 | 0.737 | 0.244 |
| Mean temperature driest quarter | 0.855 | 0.438 | −0.042 |
| Mean temperature warmest quarter | 0.658 | 0.721 | 0.190 |
| Mean temperature coldest quarter | 0.874 | 0.363 | −0.279 |
| Annual precipitation | 0.578 | −0.675 | 0.187 |
| Precipitation wettest quarter | 0.490 | −0.497 | 0.121 |
| Precipitation driest quarter | 0.347 | −0.508 | 0.661 |
| Precipitation seasonality | −0.523 | 0.581 | −0.270 |
| Precipitation warmest quarter | 0.436 | −0.466 | 0.208 |
| Precipitation coldest quarter | 0.376 | −0.585 | 0.607 |