American Journal of Botany

American Journal of Botany 99(7): 1146–1157. 2012.

Poinsettia's wild ancestor in the Mexican dry tropics: Historical, genetic, and environmental evidence[1]

Laura Trejo[2], Teresa Patricia Feria Arroyo[3], Kenneth M. Olsen[4], Luis E. Eguiarte[5], Baruch Arroyo[2], Jennifer A. Gruhn[4], and Mark E. Olson[2,6]

[2]Instituto de Biología, Universidad Nacional Autónoma de México, México DF 04510 México; [3]Department of Biology, University of Texas-Pan American, 1201 W. University Drive, Edinburg, Texas 78541 USA; [4]Department of Biology, Campus Box 1137, Washington University, St. Louis, Missouri 63130-4899 USA; and [5]Departamento de Ecología Evolutiva, Instituto de Ecología, Universidad Nacional Autónoma de México, México DF 04510 México

- *Premise of the study:* The poinsettia (*Euphorbia pulcherrima*) is the world's most economically important potted plant, but despite its preeminence it is not clear which wild populations are ancestral to the varieties cultivated around the world. Tradition holds that the U.S. envoy to Mexico J. R. Poinsett collected the progenitors of the over 300 varieties in global cultivation on an 1828 excursion to northern Guerrero State, Mexico. It is unknown whether the contemporary cultivars are descended from plants from Guerrero or whether germplasm from other parts of poinsettia's 2000 km long distribution entered into cultivation during the nearly 200 yr of subsequent poinsettia horticulture.
- *Methods:* To identify the wild populations that likely gave rise to the cultivars and test this historical account, we sequenced plastid and nuclear DNA regions and modeled poinsettia's potential distribution.
- *Key results:* The combination of nuclear and plastid haplotypes characterizing cultivars was found only in northern Guerrero. Distribution modeling indicated that suitable habitat conditions for wild poinsettias are present in this area, consistent with their likely wild status.
- *Conclusions:* Our data pinpoint the area of northern Guerrero as the cultivated poinsettia's probable ancestral region, congruent with the traditional account attributing the original collections to Poinsett. Abundant genetic variation likely offers raw material for improving the many shortcomings of cultivars, including vulnerability to cold, stem breakage, and pathogens such as *Pythium* and *Phytophthora*. However, genetic differences between populations make conservation of all of poinsettia's diversity difficult.

Key words: centers of origin; conservation; distribution modeling; domestication; *Euphorbia pulcherrima*; Euphorbiaceae; management; poinsettia.

Recognizing the places where domesticated organisms come from is a crucial aspect of studies of domestication (Zohary, 2004; Emshwiller, 2006; Zeder et al., 2006; Burger et al., 2008). It is a fundamental step in locating the ancestors of domesticates to enable study of the patterns and processes of domestication (Vilà et al., 1997; Olsen and Schaal, 1999; Larson et al., 2005; Driscoll et al., 2007; Kwak et al., 2009; Xia et al., 2009). At the same time, by identifying the wild ancestors of our domesticates, we can guide the sampling of wild germplasm for their conservation and for improvement of crops, such as via increased resistance to diseases or climate change (Harter et al., 2004; Baig et al., 2005; Miller and Knouft, 2006; Xia et al., 2009).

The search for the wild ancestors of domesticates is often hampered because so many domestications are ancient with respect to human society. Domestication of wheat, cows, barley, and pigs began more than 10 000 yr ago (Diamond, 2002; Baig et al., 2005; Haudry et al., 2007; Larson et al., 2007; Morrell and Clegg, 2007). Continual movement and habitat alteration by humans means that the original distributions of many wild species are forever erased in time (Parthasarathy, 1948; Eriksson et al., 2008; Gunn et al., 2011). For example, the predomestication distribution of the pomegranate is unknown (Kochhar, 1998), hindering management of wild germplasm. Understanding the domestication process may be obscured because selection pressures may differ over time. For example, the horse may have initially been domesticated for food and milk and only subsequently used for riding or as a beast of burden, and some have suggested that maize was initially domesticated for its sweet pithy stem (Smalley and Blake, 2003; Outram et al., 2009). For ancient domesticates, we have little choice but to face this lack of information, but fortunately many economically and culturally important organisms have been domesticated in historical times. Recently domesticated organisms provide data-rich study systems because they have often been subjected to documented selection pressures, and less time has elapsed for their wild distribution to be altered. Here we examine the origin of a recent ornamental domesticate from Mexican tropical dry forests.

[1]Manuscript received 14 February 2012; revision accepted 15 June 2012.

Funded by National Geographic Society CRE grant 8710-09 and CONACYT grant 132404. For L.T., this paper is in partial fulfillment of the requirements of the Posgrado en Ciencias Biológicas, UNAM, whose support is gratefully acknowledged, in addition to CONACYT and ICyTDF for a graduate scholarship and D. Piñero for kind guidance. The authors thank L. Small and C. León for help in the laboratory; L. Márquez and A. de Nova for support in obtaining sequences; R. Gómez, J. Rosell, J. C. Montero, M. Véliz, E. Ramírez, and A. Cervantes for support in the field; Royal Botanic Garden Edinburgh; J. Fry, R. Bye, and S. Magallón for historical information; M. Mayfield for kindly providing his invaluable monograph; and A. Bernuetz, L. Alvarado, G. Croft, V. Rojas, and G. Montes for helpful comments.

[6]Author for correspondence (e-mail: molson@ibunam2.ibiologia.unam.mx); phone: 52 (55) 5622-9124; 52 (55) 5550-1760

doi:10.3732/ajb.1200072

The poinsettia, *Euphorbia pulcherrima* Willd. ex Klotsch (Euphorbiaceae), also known as nochebuena, star of Bethlehem, or Christmas star, is the most economically important potted plant worldwide, driving annual sales in the hundreds of millions of dollars (Ecke, 2011; USDA and NASS, 2011). The plant grows wild in Mexican tropical forests, as a lanky, few-stemmed shrub or small tree. It bears its striking displays of brilliant red, or more rarely white, bracts (modified leaves surrounding the inconspicuous flowers) in the winter dry season when the plants are often leafless (Fig. 1). Compared to domesticated plants, the wild plants have tall, unbranched stems with long internodes, the bracts are much narrower and less brilliant, and the flowers and fruits are much more numerous and larger (Fig. 1A–D). Over the past 180 yr, poinsettia breeders have developed cultivars with larger bracts of various shapes and colors, and smaller, much more compact plants (Fig. 1E–H) (Moon, 1956; Ecke et al., 1990; Potter and Eames, 1997; Parks and Moyer, 2004; Ecke, 2011).

The poinsettia is a member of the eponymous subgenus within *Euphorbia*, a clade containing some 24 species (Mayfield, 1997; Steinmann and Porter, 2002). Poinsettia clade species are found in North and South America and include annual weeds (*E. cyathophora*), tuberous herbs (*E. strigosa*), shrubs (*E. cornastra*), and the largest member, the treelet *E. pulcherrima.* The species most similar morphologically to the poinsettia is *E. cornastra*, the dogwood poinsettia, endemic to a remote outcrop of limestone 1900 m high in the Sierra Madre del Sur in Guerrero, northwest of Acapulco. This species differs from *E. pulcherrima* in having a much denser, compact, shorter habit, deep green, more leathery leaves, and white bracts on inflorescences

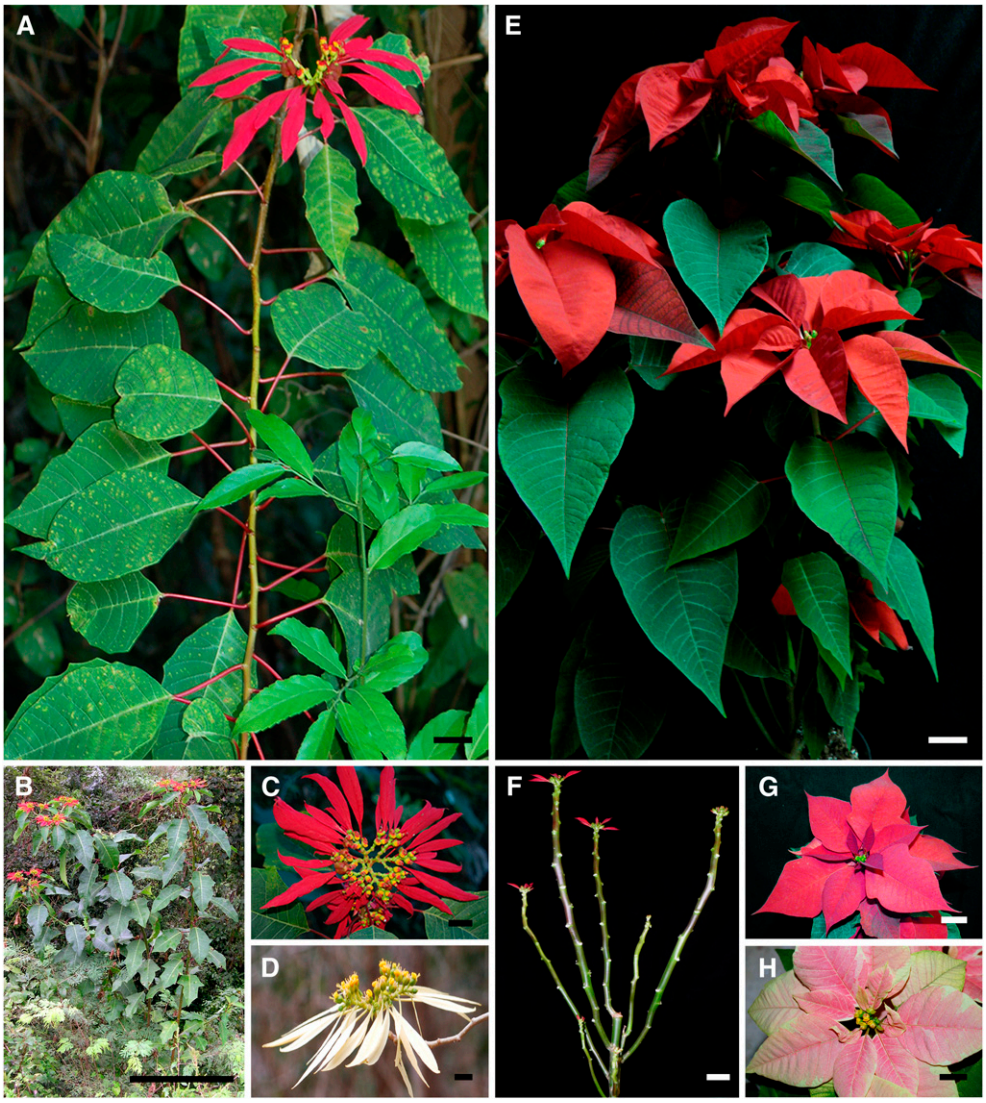

Fig. 1. Habit and flowers of wild and domesticated plants of *Euphorbia pulcherrima*. (A) Wild plant in Oaxaca, Mexico, showing the small, sparse bracts, tall habit, and long internodes of wild plants. (B) Habit of a wild plant in Guerrero, Mexico, showing the tall stature, commonly reaching 3–4 m, and the sparse branching of wild plants. (C) Inflorescence in Oaxaca, Mexico, with the abundant flowers that characterize wild plants. (D) Inflorescence with white bracts, an extremely uncommon variant. (E) Typical habit of a domesticated plant, showing the wide, abundant bracts and short internodes. (F) Domesticated plants are highly branched as compared to wild ones, as illustrated by this defoliated individual. (G) Domesticated poinsettias have very dense, more abundant bracts as compared to wild plants, few flowers, and no fruits. Some varieties are pale red or pink. (H) Some domesticated varieties are pink, white, plum-colored, or even mottled. Scale bars in A, C–H = 3 cm; in B = 1m.

that appear during the summer rainy season rather than at the height of the winter dry season. No natural hybrids are known in poinsettia, and little is known regarding interpopulational morphological variation across its range.

Identifying the population or populations that gave rise to the poinsettias cultivated worldwide would offer an essential guide for incorporating novel variation into the cultivars. Moreover, recognizing the wild germplasm from which the cultivars were derived would be useful for managing and protecting *Euphorbia pulcherrima* (Harter et al., 2004; Miller and Schaal, 2005; Spooner et al., 2005). Despite its economic importance and the utility of studies of the place of origin of the cultivars and the genetic variation within this species, little research has been conducted on this emblematic plant with respect to the origin of its worldwide commercial cultivars (Moon, 1956; Fry, 1994).

One of the advantages of studying a taxon domesticated in historical times is the written documentation that provides guidance regarding where to search for the wild ancestors. With respect to the poinsettia, historical documents indicate that the species was introduced to horticulture by Joel Roberts Poinsett, the first U. S. Minister Plenipotentiary in Mexico (Rafinesque, 1833; Graham, 1836; Moon, 1956; McGinty, 1980; Fry, 1994). In 1828, Poinsett, a member of the American Philosophical Society, traveled through Mexico with colleagues of the Philadelphia scientific community (Ronaldson, 1828; Say, 1828; Fry, 1994). On the excursion, Poinsett obtained poinsettias and sent them that same year to the Bartram Botanical Garden in Philadelphia, where they were cultivated and exhibited to the public in June of 1829 (Fry, 1994). Famed Philadelphia plantsman Robert Buist then introduced the plants grown by Bartram to Europe in 1834 (Ronaldson, 1828; Say, 1828; Rafinesque, 1833; Graham, 1836; Moon, 1956; McGinty, 1980; Fry, 1994). In contrast to poinsettia's well-documented introduction history in the United States and Europe, the geographical origin of the original wild stock is uncertain.

It is often repeated that Poinsett collected his wild plants near the town of Taxco, in the northern part of the Mexican state of Guerrero (see map in Fig. 2; McGinty, 1980; Ecke et al., 1990). Although frequently cited, there is little written evidence to corroborate this story. Poinsettia grows wild along the tropical Pacific slope in mid-elevation dry forests from northwestern Mexico to southern Guatemala over a range of some 2000 km. The original germplasm could conceivably have come from any population along poinsettia's immense range. The accuracy of the traditional story of a Guerreran origin has never been tested, and even if true, germplasm from other localities may have been incorporated into the cultivars over the past 180 yr. To test the traditional story of the origin of poinsetta, we sampled 21 populations throughout poinsettia's entire wild range and sequenced DNA from the *trnG-trnS* and *psbA-trnH* plastid regions and from the nuclear gene *G3pdh* (sequences for these primers can be found in Hamilton, 1999; Sang et al., 1997; Strand et al., 1997).

Most poinsettia populations grow on Pacific slopes, and the putative progenitors of cultivated poinsettias are unusual in that these populations occur far inland. It is known that at least as early as the 1500s, the Aztecs brought poinsettias to what is now Mexico City, most likely via northern Guerrero (Hernández, 1946, 1959; Dibble and Anderson, 1963; Navarro, 1992). This raises the question of whether the apparently wild plants in this area are actually native or whether they may be remnants of ancient horticulture. Thus, even though Poinsett could have collected his material from a canyon in the proximity of Taxco, the plants he collected may have been remnants from cultivated plants tracing their lineage to traditional horticulture. Plants of this area are often close to population centers, consistent with a hypothesis of human introduction.

One method for investigating the wild status of the inland populations is via species distribution modeling. These models correlate known geographic distribution where the species occurs (latitude/longitude) with environmental variables (climatic or topographic) predicting potential distribution or suitable habitat for the target species. The suitable habitat can then be visualized using geographic information systems. Although different factors determine the distribution of a species (e.g., interactions with other species, dispersal mechanisms, presence

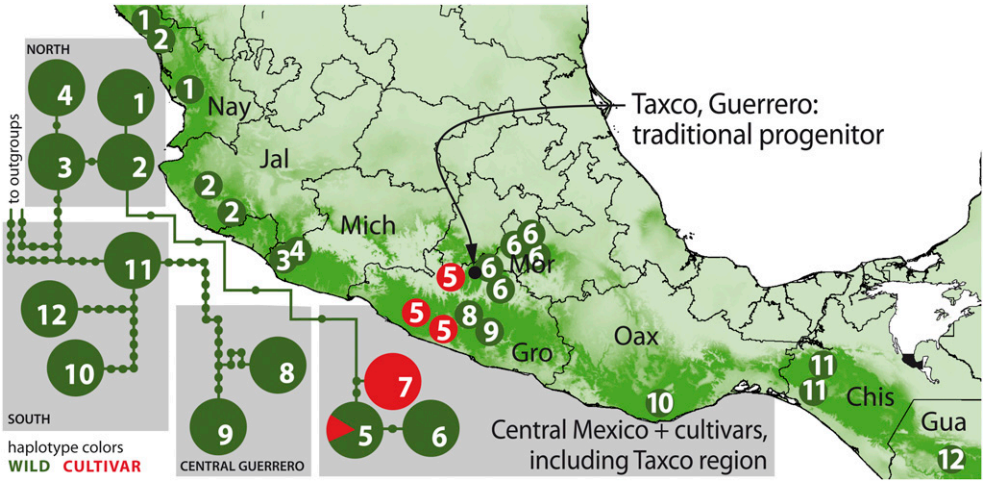

Fig. 2. Plastid haplotype network and potential distribution of *Euphorbia pulcherrima* modeled including inland populations. The plastid DNA haplotype network shows that the wild ancestors of the poinsettia likely hailed from an area ranging from southwestern central Guerrero to southern Morelos (dots = inferred mutations; numbered circles = observed haplotypes). Shading on the map denotes areas identified by species distribution modeling as having suitable poinsettia climate; the darker the shading, the greater the suitability. This model was generated based on the typical coastal populations as well as inland ones. Mexican state abbreviations north to south are as follows: Nay = Nayarit, Jal = Jalisco, Mich = Michoacán, Gro = Guerrero, Mor = Morelos, Oax = Oaxaca, Chis = Chiapas. Gua = Guatemala.

of barriers, speciation process), climatic variables such as temperature and precipitation are frequently used to estimate species distributions because they limit distributions directly by affecting growth or survival (Guisan and Zimmermann, 2000). We reconstructed poinsettia's suitable habitat using all known wild localities and also using only the typical coastal populations. Finding that the inland populations have suitable poinsettia habitat would make their wild status more plausible. In contrast, if we were to find that the inland populations grow in areas that are entirely unlike the coastal populations in their climate regimes, then this would make their wild status seem less likely and increase suspicion that they are remnants of cultivation. Mapping poinsettia distribution also provides an essential guide for conservation.

Using our species distribution maps, we assessed the level of conservation risk of wild populations of *Euphorbia pulcherrima* in Mexico, where development is fragmenting its original wild distribution. Poinsettia grows in tropical dry forests, where deforestation is largely unchecked (Mas et al., 2004). Understanding the ecological and geographical distribution of poinsettia is essential for improving management and conservation efforts. We provide an assessment of the protection status of wild poinsettia in Mexico by identifying populations growing in protected areas. In tandem with these efforts, characterizing the geographical distribution of genetic variation is essential for locating priority areas for conservation of the greatest genetic variation or unique variants (Arriaga et al., 2000; CEUM, 2011).

Recognizing centers of origin of domesticated organisms is fundamental for understanding the evolutionary process of domestication, and essential for improving management and conservation of natural resources. Multiple sources of data should lead to more robust inferences of centers of origin. We present an example of such an exercise by integrating three sources of evidence: historical, genetic, and ecological. The objectives of this study were (1) to identify the wild populations that gave rise to one of the world's most important ornamental plants, the poinsettia, (2) to evaluate the possibility that poinsettia populations were introduced from the Pacific Coast to central Mexico, (3) to assess preliminarily the state of conservation of poinsettia in the wild, and (4) to propose basic guidelines for designing management strategies for wild germplasm of Mexican poinsettia. The information generated by our study can provide the foundation for a better utilization of this plant of global economic and cultural importance.

MATERIALS AND METHODS

***Plant collections*—**We sampled 21 populations of *Euphorbia pulcherrima*, comprising 65 individuals from throughout the plant's entire wild range in mid-elevation tropical dry forests from northwestern Mexico to southern Guatemala. In addition, we included 14 major commercial poinsettia cultivars from the United States and Mexico (Table 1). We used as outgroups *Euphorbia cornastra* (Dressler) Radcliffe-Smith, poinsettia's likely sister taxon, and *E. heterophylla* L., a widespread annual that is also a member of subgenus *Poinsettia* (Mayfield, 1997; Steinmann and Porter, 2002; Zimmermann et al., 2010).

***DNA extraction, PCR amplification, and DNA sequencing*—**We extracted DNA from fresh or silica gel-dried leaf samples (Table 1) with DNeasy Plant Mini Kits (Qiagen, Valencia, California, USA) and PCR amplified two plastid intergenic spacers, *trnG*$^{(UCC)}$-*trnS*$^{(GCU)}$ (Hamilton, 1999) and *psbA-trnH* (Sang et al., 1997). The protocol for *trnG-trnS* was 80°C/5 min; 29 cycles of 95°C/1 min, 66°C/4 min, followed by one cycle of 66°C/10 min and finally one cycle of 10°C/10 min. For *psbA-trnH*, cycling conditions were 94°/2 min, followed by 30 cycles 94°C/45 s, 52°C /1 min and 72°C/75 s, and finally an elongation period of 72°C/7 min.

Our final PCR amplifications had volumes of 50 μL, with each reaction containing 10–100 ng of DNA and the following reagents and proportions: 5 μL 10× of buffer, 1 μL of 10 μmol/L dNTPs in an equimolar ratio, 1.5 μL (*trnG–trnS*) or 0.8 μL (*psbA-trnH*) of 50 μmol/L $MgCl_2$, 1 μL of 10 μM primer, and 1 unit of *Taq* polymerase. We purified PCR products with QIAquick PCR purification kits (Qiagen), and sequenced them bidirectionally using BigDye Terminator (Applied Biosystems, Foster City, California, USA) in final volumes of 10 μL. We cleaned the labeled products with Sephadex G-50 (GE Healthcare Bio-Sciences, Piscataway, New Jersey, USA) and sequenced them on an ABI 3 100 sequencer (PE Biosystems). We used the program Sequencher v4.7 (Gene Codes, Ann Arbor, Michigan, USA) to edit the sequences and aligned them by eye using the program Se-Al v.2.0a11 Carbon (Rambaut, 2002).

We designed specific primers for *E. pulcherrima* to amplify the low-copy number nuclear gene encoding glyceraldehyde 3-phosphate dehydrogenase (*G3pdh*) based on the primers GPDX7F and GPDX9R of Strand et al. (1997). The forward primer sequence (01F) was 5′ ACT GTC CAT TCC ATT ACT GGT AA 3′. The reverse primer sequence (01R) was 5′ ACT TGA TCT GCA ACA ATA AGT CAT 3′. The PCR protocol started at 95°C/1 min; followed by 35 cycles of 95°C/1 min, 53°C/1 min, and 72°C/90 s; with a final elongation period of 72°C/7 min. We carried out a 25 μL reaction per individual, each reaction containing 5 μL of 5× GoTaq buffer, 1.5 μL of 25 μmol/L $MgCl_2$, 1 μL of 10 μmol/L primer, and 0.5 units of GoTaq polymerase (Promega, Madison, Wisconsin, USA). We visualized PCR products on 1% agarose gels and subsequently, we used pGEM-T Easy Vector System from Promega and inserted amplified fragments in DH5-alpha competent cells using the FSB method (Sambrook et al., 1989). The insert was sequenced using M13F and M13R vector primers, and we cloned three sequences per individual in both directions to obtain one unambiguous DNA sequence haplotype per individual.

***Relationships among wild plants and cultivars*—**To infer relationships, we constructed haplotype networks and rooted trees, giving us the framework necessary for comparing the genetic variants (haplotypes) of the cultivars to the wild plants. We explored the congruence between loci by the incongruence length difference (ILD) test (Farris et al., 1994), as implemented in the program WinClada version 1.00.08 (Nixon, 2002), running 1000 replicates ($P = 1.00$, W and S = 1000). We treated gaps as missing data for all analyses. We constructed statistical parsimony networks using a 95% connectivity limit in the program TCS 1.21 (Clement et al., 2000), one for the nuclear DNA sequences alone, and another for the combined plastid regions given that the patterns recovered from the two regions sequenced were highly congruent with one another (see Results). For parsimony and Bayesian phylogenetic analyses, we analyzed separately the plastid and nuclear loci before performing a combined analysis of the plastid and nuclear regions for the individuals for which all three loci were available. For parsimony analyses, we coded characters as unordered and gave them equal weights. We conducted parsimony heuristic searches using the program Nona 2.0 (Goloboff, 1999), performing 10 different searches. A total of 5000 random addition sequences in sets of 1000 seeds were submitted to tree-bisection-reconnection (TBR) branch swapping, holding 100 trees. We saved the most parsimonious trees, removed identical trees, and calculated a strict consensus using the Nelsen command in WinClada v. 1.00.08 (Nixon, 2002). We plotted the support values from 1000 bootstrap replicates on the SC tree that resulted from analysis of all of the data. Finally, we used Bayesian phylogenetic methods to describe the pattern of relationships among individuals of *Euphorbia pulcherrima*. We determined the model of evolution that best fit our data using the Akaike information criterion (Akaike, 1974) as implemented in the program ModelTest v.3.7 (Posada and Crandall, 1998). For Bayesian analysis, we partitioned the loci and ran four Markov chains for 40 000 000 generations using a heating parameter of 0.04 in MrBayes v. 3.1.2 (Huelsenbeck and Ronquist, 2001). Using the same software, we also performed an analysis of the combined plastid regions, and a third one with *G3pdh* alone, having run for each of them four Markov chains for 10 000 000 generations. The heating parameters were 0.02 for the plastid regions and 0.04 for *G3pdh*. We confirmed stationarity in graphs of log-likelihood scores vs. generation, discarding the initial 25% of the trees as burn-in and calculating a consensus with the remaining ones. We excluded half of the trees before calculating the Bayesian posterior probabilities (PP).

Finally, using the program ARLEQUIN 3.1 (Excoffier et al., 2005), we performed a Mantel test with 10 000 permutations to evaluate correlations between linear geographic distances and genetic distances across all localities. We delimited the likely ancestral area of the cultivated poinsettia by identifying the minimal set of wild populations that included the cultivar haplotypes (Gaskin and Schaal, 2002).

TABLE 1. Voucher information (all at MEXU), haplotype number, and GenBank accession numbers of the samples sequenced; states are Mexican except for Sacatepéquez, which is in Guatemala, while cultivars are commercial horticultural varieties from nurseries.

State / Species	Collection no.	Source / Cultivar	Haplotype$_{cp}$[a]	Haplotype$_{n}$[b]	*psbA-trnH*	*trnG-trnS*	*G3pdh*
E. pulcherrima	1071-10	Sinaloa	1	4	HM155953	HM156016	JN613195
E. pulcherrima	1071-55	Sinaloa	1	9	HM155954	HM156017	JN613210
E. pulcherrima	1073-9	Nayarit	1		HM155955	HM156018	
E. pulcherrima	1073-16	Nayarit	1	1	HM155956	HM156019	JN613177
E. pulcherrima	1076-13	Jalisco	2	10	HM155948	HM156011	JN613222
E. pulcherrima	1076-39	Jalisco	2	1	HM155949	HM156012	JN613183
E. pulcherrima	1071A-16	Sinaloa	2	10	HM155950	HM156013	JN613218
E. pulcherrima	1071A-18	Sinaloa	2	9	HM155951	HM156014	JN613217
E. pulcherrima	1071A-26	Sinaloa	2	1	HM155952	HM156015	JN613182
E. pulcherrima	62-10	Jalisco	2	2	HM155975	HM156038	JN613188
E. pulcherrima	62-31	Jalisco	2		HM155976	HM156039	
E. pulcherrima	1085-17	Michoacán	3	1	HM155957	HM156020	JN613181
E. pulcherrima	1085-22	Michoacán	3	9	HM155958	HM156021	JN613213
E. pulcherrima	1086-11	Michoacán	4		HM155959	HM156022	
E. pulcherrima	1086-15	Michoacán	4		HM155960	HM156023	
E. pulcherrima	8-10	Guerrero	5		HM155925	HM155988	
E. pulcherrima	8-20	Guerrero	5		HM155926	HM155989	
E. pulcherrima	8-21	Guerrero	5	6	HM155927	HM155990	JN613203
E. pulcherrima	11-3	Guerrero	5		HM155928	HM155991	
E. pulcherrima	11-23	Guerrero	5	5	HM155929	HM155992	JN613201
E. pulcherrima	114-4	Guerrero	5	5	HM155930	HM155993	JN613202
E. pulcherrima	114-16	Guerrero	5	2	HM155931	HM155994	JN613186
E. pulcherrima	114-20	Guerrero	5	2	HM155932	HM155995	JN613187
E. pulcherrima	64-15	Guerrero	6	3	HM155935	HM155998	JN613193
E. pulcherrima	64-34	Guerrero	6	10	HM155936	HM155999	JN613223
E. pulcherrima	64-35	Guerrero	6	7	HM155937	HM156000	JN613206
E. pulcherrima	115-7	Guerrero	6	1	HM155940	HM156003	JN613178
E. pulcherrima	115-9	Guerrero	6	1	HM155941	HM156004	JN613180
E. pulcherrima	115-32	Guerrero	6	1	HM155942	HM156005	JN613179
E. pulcherrima	68-6	Morelos	6		HM155933	HM155996	
E. pulcherrima	68-15	Morelos	6	4	HM155934	HM155997	JN613196
E. pulcherrima	107-13	Morelos	6	7	HM155938	HM156001	JN613208
E. pulcherrima	107-15	Morelos	6	3	HM155939	HM156002	JNG13227
E. pulcherrima	1257-1	Morelos	6	10	JQ666170	JQ666172	JN613225
E. pulcherrima	1257-2	Morelos	6	10	JQ666171	JQ666173	JN613226
E. pulcherrima	104-1	Guerrero	8	10	HM155970	HM156033	JN613219
E. pulcherrima	104-9	Guerrero	8		HM155971	HM156034	
E. pulcherrima	104-13	Guerrero	8	9	HM155972	HM156035	JN613212
E. pulcherrima	60-31	Guerrero	9	2	HM155967	HM156030	JN613190
E. pulcherrima	60-18	Guerrero	9	6	HM155968	HM156031	JN613205
E. pulcherrima	60-44	Guerrero	9	2	HM155969	HM156032	JN613191
E. pulcherrima	18-48	Oaxaca	10	6	HM155973	HM156036	JN613204
E. pulcherrima	18-50	Oaxaca	10	9	HM155974	HM156037	JN613211
E. pulcherrima	1106-4	Chiapas	11	5	HM155965	HM156028	JN613198
E. pulcherrima	1106-11	Chiapas	11	4	HM155966	HM156029	JN613197
E. pulcherrima	1108-29	Chiapas	11	9	HM155963	HM156026	JN613214
E. pulcherrima	1108-37	Chiapas	11	10	HM155964	HM156027	JN613224
E. pulcherrima	56-4	Sacatepéquez	12	10	HM155961	HM156024	JN613220
E. pulcherrima	56-9	Sacatepéquez	12	3	HM155962	HM156025	JN613192
E. pulcherrima	74	Freedom Red	5		HM155916	HM155979	
E. pulcherrima	47	Rosa	5		HM155917	HM155980	
E. pulcherrima	73	Sup-Jibi	5	3	HM155918	HM155981	JN613194
E. pulcherrima	75	V-10 Marble	5	5	HM155919	HM155982	JN613199
E. pulcherrima	55	Silverstar Marble	5	1	HM155920	HM155983	JN613184
E. pulcherrima	37	Red Glitter	5	10	HM155921	HM155984	JN613221
E. pulcherrima	45	Festival White	5	1	HM155922	HM155985	JN613185
E. pulcherrima	117	Nutcracker Salmon	5	2	HM155924	HM155987	JN613189
E. pulcherrima	123	Carrousel Dark Red	5		HM155923	HM155986	
E. pulcherrima	39	Uva	7	7	HM155947	HM156010	JN613207
E. pulcherrima	52	Rehilete	7	9	HM155944	HM156007	JN613215
E. pulcherrima	76	Marble Star	7		HM155945	HM156008	
E. pulcherrima	118	Valenciana	7	9	HM155943	HM156006	JN613216
E. pulcherrima	44	Rosa Moteada	7	9	HM155946	HM156009	JN613200
E. pulcherrima	61	Guerrero	13		HM155977	HM156040	
E. pulcherrima	63	Jalisco	14	8	HM155978	HM156041	JN613209

[a]Plastid haplotypes (Haplotype$_{cp}$) numbers correspond to those in Fig. 2.
[b]Nuclear haplotypes (Haplotype$_{n}$) numbers correspond to those in Fig. 3.

***Suitable habitat for poinsettia in Taxco and Morelos*—**To explore the hypotheses that the northern Guerrero populations could be native or might more plausibly represent human introductions, we estimated the potential distribution of *E. pulcherrima*. As understood here, potential distribution is the geographical extent of its suitable habitat, the climatic conditions it typically occupies. We used the program MaxEnt v. 3.3.3e (Phillips et al., 2004, 2006, Phillips, 2008) with the default modeling parameters and 19 bioclimatic variables drawn from the WORLDCLIM database (http://www.worldclim.org; Hijmans et al., 2005) as environmental predictors. We generated models based on presence records including 22 of our own field collections (Table 1) and 15 localities obtained from herbarium specimens. Our model of potential distribution had a spatial resolution of 0.008° (~1 × 1 km). We processed the resulting models using the program ArcGIS 10 (ESRI, Redlands, California, USA) and evaluated model predictability calculating the area under the curve (AUC) in receiver operating characteristics plots (Fielding and Bell, 1997). We divided the presence data, using 70% to train the model and 30% to evaluate it 100 times. The final model was the average of the 100 replicates, and thus the resulting AUC is also the average. Modeling potential distribution allowed us to characterize the combinations of climatic variables at wild poinsettia localities and to identify sites between them with prospects of having similar combinations and thus poinsettias.

***Conservation of wild poinsettia*—**For a first approximation to determine the conservation status of wild poinsettia, we assessed which populations are safeguarded in protected areas. We compared the potential distribution map of poinsettia with the Protected Natural Areas (PNAs) and Priority Terrestrial Regions (PTRs) of Mexico. PNAs are portions of Mexican territory significant for their high biodiversity, ecological and social benefits, and potential for conservation (Arriaga et al., 2000; CEUM, 2011). PTRs are areas of high richness and endemism, but they are not afforded any protection (Solano and Feria, 2007). In addition, we used the human footprint map of Sanderson et al. (2002) to estimate the impact of human activities on wild populations (see Feria Arroyo et al., 2009). This index assigns an impact value to pixels worldwide based on proximity to sources of disturbance. The human footprint is derived from a 1 × 1 km raster data set produced by compiling scores from population density, land transformation, accessibility, and power infrastructure data to generate an estimate of human impact ranging from 0 to 100, with 0–10 being wildlands and the most transformed habitats approaching 100 (Sanderson et al., 2002). To generate maps of PNAs, PTRs, and human footprint scores, we analyzed the intersections of geographic data with the polygons of the ANPs, RTPs, and raster of HF in ArcGIS 10 (ESRI, Redlands, California) using Hawths tools (http://www.spatialecology.com/htools). Our map allowed us to identify which haplotypes are present in PNAs or RTPs and the degree of human influence in those areas.

RESULTS

***Relationships among wild plants and cultivars*—**We obtained DNA sequences from 51 to 65 individuals from 20 to 21 populations, depending on the marker (Table 1). Sequences of the plastid *psbA-trnH* spacer resulted in a multiple alignment of 716 bp, *trnG-trnS* 838 bp, and *G3pdh* 770 bp. GenBank accession numbers are given in Table 1 and the alignments are available as TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S11968).

Statistical parsimony networks (Templeton et al., 1992; Clement et al., 2000) recovered 12 plastid haplotypes for *Euphorbia pulcherrima*, 11 of which were in wild populations and two in cultivars (Table 1). Nine of the 14 cultivars sampled had haplotype 5, which was also present in wild populations of northern and western Guerrero. The other five cultivars had haplotype 7, which was not detected in wild populations but was genealogically very close to haplotypes 5 of Guerrero and 6 of northern Guerrero and Morelos, with which it forms a small clade ("Central Mexico" in Fig. 2). "North" was made up of populations from Sinaloa, Nayarit, Jalisco, and Michoacán (haplotypes 1–4). "South" comprised populations from Oaxaca, Chiapas, and Guatemala, with haplotypes 10–12. The clade "Central Guerrero" was highly localized and included populations with haplotypes 8 and 9.

In the case of the nuclear gene haplotype network, the wild populations had nine haplotypes. Most of these, in contrast to the plastid haplotypes, were widespread, and seven of them were shared with the cultivars. Nuclear haplotypes of cultivars were shared with most wild populations, but only populations from northern Guerrero, the area that includes Taxco, had all of the nuclear haplotypes found in the cultivars (Fig. 3).

The rooted tree based on the combined analysis of all loci produced largely congruent tree topologies in the MP and Bayesian analyses, with commensurate bootstrap and posterior probabilities supporting population divergences (Fig. 4). The model of molecular evolution that best fit each data set (Akaike, 1974; Posada and Crandall, 1998) was K81uf+G for *trnG-trnS*, TVM+G for *psbA-trnH*, and K81uf+I for *G3pdh*. For plastid sequences, parsimony analyses generated 85 equally parsimonious trees (length = 80, CI = 0.88, RI = 0.97), with 3.2% of the characters being parsimony informative. For plastid sequences, we recovered 20 equally parsimonious trees (length = 80, CI = 0.88, RI = 0.97), with 3.2% of the characters being parsimony informative. Analysis of nuclear sequences resulted in 40 equally parsimonious trees (length = 28, CI = 0.89, RI = 0.99) based on 3.8% parsimony informative characters. The joint analysis of all three regions produced 330 equally parsimonious trees (length = 184, CI = 0.45, RI = 0.82), with 3.2% informative characters. A 1000 replicate ILD test suggested congruence between the two plastid intergenic spacers ($P = 0.999$) and significant incongruence between plastid and nuclear sequences ($P = 0.001$).

The rooted trees based on the combined plastid markers had four main clades. The cultivars were found in one of these clades, "Central Mexico" (PP = 1, PB = 82), which was made up of poinsettia cultivars and wild populations from Morelos to western Guerrero (Fig. 4A). The northernmost populations of *E. pulcherrima*, from Sinaloa to Michoacán, made up the "North" clade (PP = 1, PB = 87). Populations from Oaxaca, Chiapas, and Guatemala made up the "South" clade (PP = 0.93, PB = 58), while the populations of central Guerrero are again isolated in their own clade (PP = 1, PB = 90). Tree reconstructions based only on the nuclear gene and combined nuclear and plastid markers did not reveal any clear association between clades and geographical regions (the combined tree is shown in Fig. 4B). Regardless of the geographic patterns of associations of the clades, the combination of nuclear and plastid haplotypes present in cultivars was found only in a small area from northern Guerrero, making this region the most plausible source of the ancestors of poinsettia cultivars (Fig. 3). Mantel tests suggested that *E. pulcherrima* lacks a significant pattern of isolation by distance, whether in an analysis of the combined nuclear and plastid regions ($r = 0.10$; $P = 0.22$), plastid sequences ($r = 0.20$; $P = 0.10$), or the nuclear region ($r = -0.01$; $P = 0.48$; Excoffier et al., 2005).

***Suitable habitat for poinsettia of Taxco*—**The area under the curve (AUC) from the training runs was 0.98 and from testing 0.96. The maps depicting the geographical extent of poinsettia's suitable habitat show favorable areas all along the tropical Pacific coast of Mexico as well as in inland Guerrero and southern Morelos States (Fig. 2). When we modeled poinsettia's suitable habitat based only on typical populations from the Pacific slope, we continued to recover high probabilities of finding poinsettia habitat in northern Guerrero and Morelos (Fig. 3). Checking the accuracy of these predictions via field visits to areas of high model predictivity but with no known collections

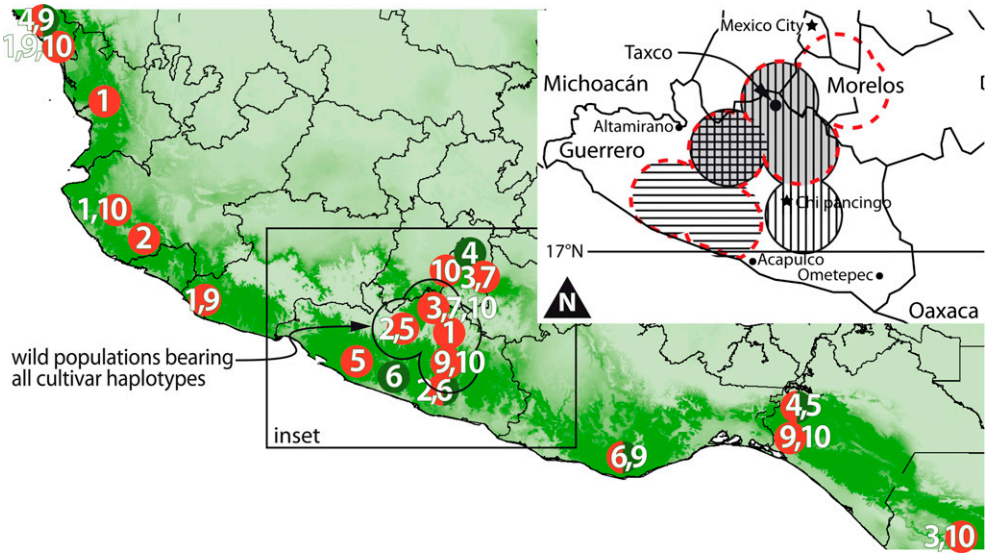

Fig. 3. Geographical distribution of *G3pdh* nuclear haplotypes and potential distribution of *Euphorbia pulcherrima* based only on typical populations from the Pacific slope. The numbered circles are observed haplotypes: red denotes populations with one or more haplotype shared with the cultivars; green indicates populations with no cultivar haplotype. Suitable habitat for poinsettia is found in the putative ancestral region of northern Guerrero, even when these populations are not included as the basis for modeling potential distribution. This result is congruent with the notion that populations in this area are indeed wild. The rounded polygon (arrow) outlines the extent of populations that include all seven haplotypes found in cultivars. This region falls only in central northern Guerrero. Inset: The geographical extent of the clade containing the three "Central Mexico" plastid haplotypes of Fig. 2 is outlined with a dotted line. Plastid haplotype 5 (Fig. 2) populations are shown in horizontal hatching. The extent of the region in which all of the cultivar nuclear haplotypes is found is shown with vertical hatching; the overlap between these regions is shaded in gray, and it is this region, as the overlap between the "Central Mexico" clade and the nuclear haplotypes, that we take to be the likeliest source region for ancestral poinsettia germplasm. This region includes Taxco, congruent with the traditional Poinsett story.

led us to previously unknown populations, including the Michoacán populations and the northern haplotype 5 locality (Fig. 2).

***Conservation of wild poinsettia*—**The distribution map (Fig. 5) shows high fragmentation of natural areas where poinsettia populations are found. Of these populations, four are likely extinct based on our fieldwork. Nineteen percent of the 21 wild poinsettia populations sampled occur in Protected Natural Areas (PNAs; Fig. 5), and include just four of the 12 plastid haplotypes (33%; Table 2). These protected populations do not include any plastid haplotypes present in the cultivars. In the case of the nuclear gene data set, six of 10 *G3pdh* haplotypes (60%) are found within PNAs, with four of them being present in cultivars (40%; Table 2). In the case of Priority Terrestrial Regions (RTRs; Fig. 5), 57% of poinsettia populations occur within them.

We obtained human impact scores for 21 wild populations (Table 2). Scores ranged from 21 to 60, with an average of 34. The index ranges from 0 to 100: 0–10 are wildlands; near 100 are the most transformed habitats (Sanderson et al., 2002). The populations most affected by human activities are near metropolitan areas, such as Taxco. We identified unique characteristics of wild populations that we consider significant for conservation. These features include plants with white bracts, small population sizes, and the occurrence of unique DNA sequence haplotypes (Table 2).

DISCUSSION

Through the study of centers of origin, we may recognize the patterns left behind by organisms during their domestication, and identifying wild relatives can guide management and conservation strategies (Kwak et al., 2009). Poinsettia is an excellent case study in recent domestication because it has been selected as an ornamental plant through intensive breeding in just over 180 yr and because the species retains much of its wild distribution. We used historical, genetic, and environmental evidence to investigate the origin of poinsettia cultivars.

Our genetic analyses support the Poinsett story, according to which the ancestors of poinsettia cultivars were collected in the vicinity of Taxco in northern Guerrero, Mexico (Moon, 1956; McGinty, 1980; Ecke et al., 1990). Individually, the plastid and nuclear data broadly help delimit poinsettia's center of origin (Figs. 3, 4A). Taken together, however, they more precisely locate the likely source of ancestral germplasm. Cultivars had two plastid haplotypes. One of them, haplotype 5, was shared with the populations of northern and western central Guerrero (Table 1, Figs. 2, 4). The other plastid haplotype found in cultivars, haplotype 7 (Table 1), was not found in any wild population but was closely related to populations from Guerrero and Morelos (Fig. 2). The nuclear data also supported the Poinsett story. Cultivars had 7 of the 9 wild nuclear haplotypes (Figs. 3, 4, Table 1). Nuclear haplotypes of cultivars were shared with most wild populations, but only populations of northern Guerrero, which includes the Taxco region, had all the haplotypes found in the cultivars. In no other region do we find so many cultivar nuclear haplotypes as in northern Guerrero, seven in four populations. For example, in the three populations of Morelos State, immediately adjacent to northern Guerrero (Fig. 3), we find just three cultivar nuclear haplotypes, as compared to seven. Across the five northernmost populations, separated by up to 450 km from Sinaloa to Jalisco, we find just four cultivar nuclear haplotypes. Similarly, over the more than 600 km spanning the four southernmost populations, from Oaxaca to Guatemala,

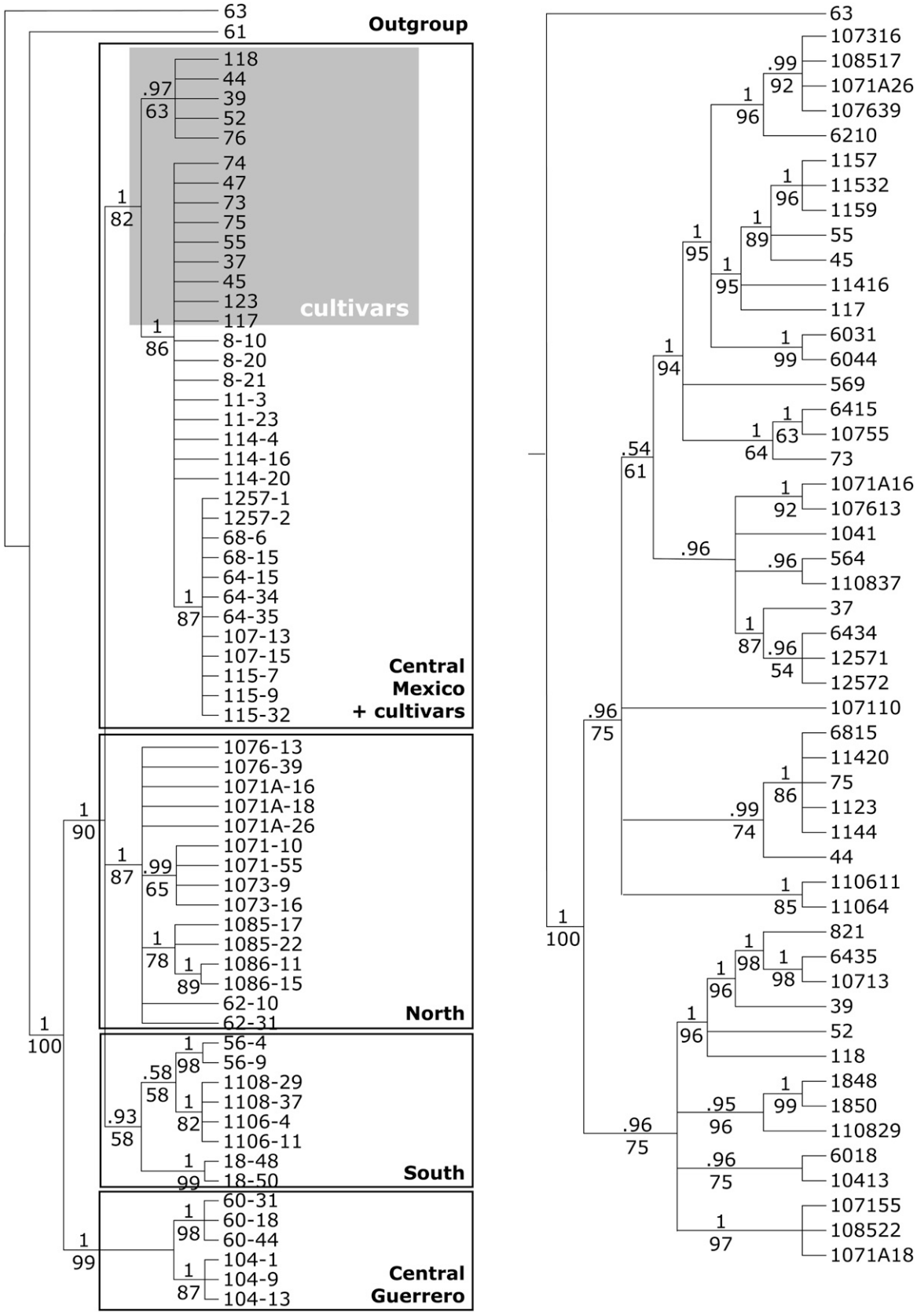

Fig. 4. Bayesian 50% majority-rule consensus cladograms based on *psbA-trnH* and *trnG-trnS* (left), and the combined plastid + nuclear data (right). Posterior probabilities are shown above branches; parsimony bootstrap values are below branches.

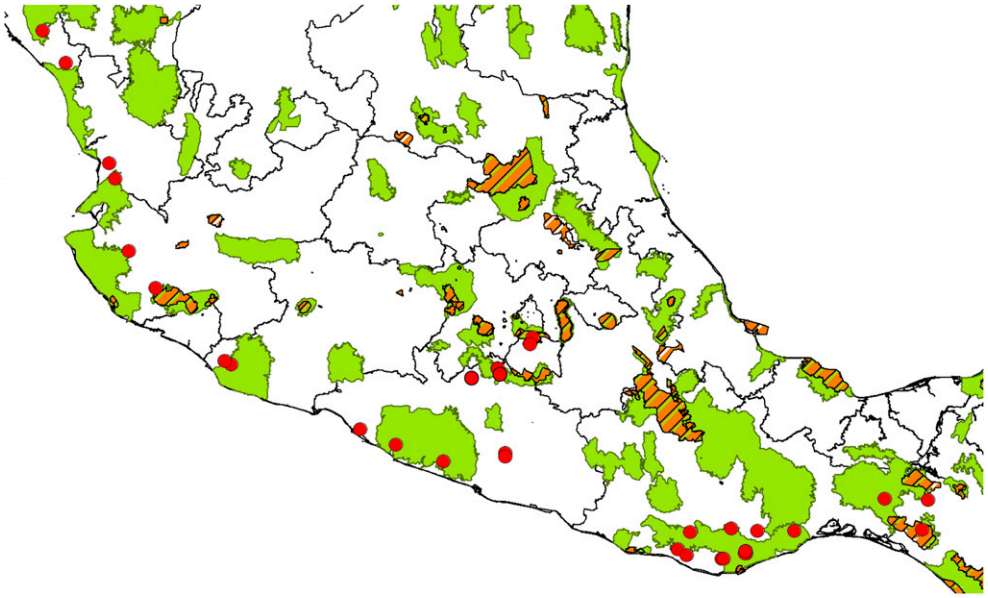

Fig. 5. Distribution of wild populations *Euphorbia pulcherrima* (red points) within Protected Natural Areas (hatching) and Priority Terrestrial Regions (green) of Mexico. Very few populations are found in protected areas.

we also find only four cultivar nuclear haplotypes. The concentration of all cultivar nuclear haplotypes in northern Guerrero and in no other part of the range strongly points to this area as the source of the ancestral poinsettia cultivar germplasm. We can overlap, Venn diagram style, the polygons enclosing on the one hand the cultivar plastid haplotypes, and on the other the one encircling the full diversity of cultivar nuclear haplotypes. Doing so reveals a tightly circumscribed region in northern Guerrero (Fig. 3). These results concur remarkably with the traditional story in which Poinsett collected the cultivated poinsettia's ancestral germplasm in the region of Taxco.

TABLE 2. Parameters referring to the conservation status of wild poinsettia populations.

Population [a]	Haplotype in PNAs [b]	HF [c]	Unique features [d]
1071		30	
1073		24	
1076		27	
1071A		30	small number of individuals
62	$H_{cp}2$, H_n2	30	
1085		29	white bracts, unique H_{cp}
1086		21	unique H_{cp}
8		35	ancestral
11		23	ancestral
114		22	ancestral
64		49	historical
115		49	historical
68	$H_{cp}6$, H_n4	60	near metropolitan area
107	$H_{cp}6$, H_n3, H_n7	60	near metropolitan area
1257		56	near metropolitan area
104		30	unique H_{cp}
60		30	unique H_{cp}
18		28	unique H_{cp}
1106		30	
1108	$H_{cp}11$, H_n9, H_n10	23	
56		34	

[a] Wild poinsettia populations (See Table 1).

[b] Plastid haplotypes (H_{cp}) and nuclear haplotypes (H_n) in Protected Natural Areas (PNAs).

[c] Human footprint (Sanderson et al., 2002) (0–10 wildlands; near 100, most transformed habitats).

[d] Unique features of wild poinsettia populations important for conservation.

These apparently ancestral northern Guerrero populations are somewhat anomalous, in that only these populations are found so far inland out of the entire range of poinsettia. Moreover, populations in this area are adjacent to or even surrounded by urban centers, observations that have led many to suppose that these populations may represent remnants from cultivation rather than truly wild plants. Our genetic evidence does not support the idea that the populations from northern Guerrero are remnants or escapes from cultivation because the populations in these areas have unique combinations of haplotypes. If they were brought from elsewhere, then we would expect them to have haplotypes reflecting the source populations. Instead, the northern Guerrero populations show patterns of geographical structuring and diversity in line with the patterns of haplotype distribution of the rest of the species. A remaining question was whether the poinsettia habitats of northern Guerrero are anomalous climatically, given their distance from typical habitats of the Pacific coast. When we modeled potential distribution based only on typical populations from the Pacific slope, we recovered high probabilities of finding poinsettia habitat in northern Guerrero and Morelos (Fig. 3). Our field visits to test the accuracy of these predictions led us to several previously undocumented populations, including the northern population of the ancestral haplotype 5 (Fig. 2). The remoteness of this locality makes its wild status almost certain. Species distribution modeling results together with our genetic data and historical accounts suggest that the wild progenitors of the poinsettias cultivated worldwide came from this area, probably collected by Poinsett nearly 180 yr ago.

***Domestication and applied uses*—**Wild poinsettias are sporadically brought into cultivation in the villages adjacent to wild populations. We have observed wild poinsettias in villages

in southern Sinaloa, the southern Sierra of Guerrero, and in southern Oaxaca. However, all of these plants had been brought into cultivation by the idiosyncratic efforts of single individuals and were not part of any local domestication efforts. Poinsettias are universally grown in the communities of poinsettia country, but they are almost always commercial domesticates from industrial horticulture. Contamination of local stands of poinsettia seems a latent risk, but fortunately most cultivars flower sparingly and do not fruit. We observed no evidence of gene flow from cultivars to wild plants.

Likewise, there seems to be limited gene flow between wild poinsettia populations. Shockingly, for such an important plant, nothing is known about pollination in poinsettia. Although we have occasionally observed wasps on the cyathia, visitors seem rare, and it is not clear how far poinsettia pollen may be carried by vectors. Poinsettia habitats are highly restricted, usually on steep slopes in canyons, with populations numbering from a few hundred but usually smaller, sometimes just a dozen or so individuals. With regard to seed dispersal from canyon to canyon, it is hard to see how the dehiscent capsules of the plant, which eject the large seeds at most a few meters, could account for dispersal over long distances. That poinsettia populations are small and have no obvious means of gene exchange between them seems congruent with our results and is more consistent with fragmentation of a formerly more continuous range rather than ongoing gene flow. The lack of a detectable pattern of geographical isolation by distance seems congruent with this notion. Whatever the origin of these patterns, the small populations scattered across the rugged Mexican landscape (Marshall and Liebherr, 2000; McCormack et al., 2008) would seem to offer abundant genetic variation that could be of applied use.

The applied importance of germplasm diversity is made clear by the manifold problems growers face in producing poinsettias. Breeders constantly strive for new cultivars with better resistance to cold, pests, stem breakage, and fungal infection (Potter and Eames, 1997; Parks and Moyer, 2004; Ecke, 2011). A major goal of new cultivar development is to address these problems (Potter and Eames, 1997; Ecke, 2011; Taylor et al., 2011). Cold resistance is a major issue, both for maintenance in the home and garden, as well as for reducing the cost of heating greenhouses. Poinsettias tend to be fragile, with branches that are relatively stiff but easily broken, weeping their white latex over the rest of the plant and any decorative potting. Plants with larger, more abundant and more colorful bracts are always desirable, especially those that are resistant to dropping their bracts or to infections such as *Botrytis* (Potter and Eames, 1997; Ecke, 2011; Taylor et al., 2011). Losses account for at least 9% of total production and mean that growers must sell 2.5 plants to make up for each lost one (Ecke, 2011). Major growers have noted that genetic improvement is one of the key factors in increasing productivity (Ecke, 2011), making understanding poinsettia genetic diversity all the more important. Features that may be of crucial interest for breeding include potentially cold-resistant populations at over 1000 m in central Mexico, populations growing in direct sun in the west, those growing on dry limestone, or variants in size and color, such as populations with white bracts (Fig. 1).

Natural variation would seem to offer many potential solutions to these problems. The species spans a marked latitudinal and elevational range and also seems to vary abundantly within populations. For example, in each population there usually seem to be individuals that maintain their bracts longer than others. If this variation were heritable, it would clearly be useful for breeding. Our results show that if nurserymen have made additional collections of wild poinsettia, they have done so from closely related haplotypes from Guerrero or Morelos and have not injected novel variation into the cultivar. Our results thus provide an essential guide for the informed enrichment of the cultivars.

Conservation status and gene flow in wild poinsettia— Despite its global economic and cultural importance, and although its populations are threatened by habitat destruction, *Euphorbia pulcherrima* is not protected under Mexican law. Our fieldwork documented the disappearance of populations from the Mexican states of Jalisco, Nayarit, and Morelos, as well as in Guatemala. Our genetic data may also suggest lost populations because we did not find plastid haplotype 7, known only from cultivars, in any wild population. This apparent absence may be filled with more intensive sampling, but given the long history of human disturbance of northern Guerrero and southern Morelos, it would not be surprising to find that the population or populations bearing this haplotype have been extirpated in ways similar to the destroyed populations we documented in Jalisco, Nayarit, Morelos, and Guatemala. The loss of poinsettia populations likely means the loss of unique genetic variants. Population differentiation might be associated with adaptive and even commercially significant interpopulational divergence. If there are no directed strategies for the conservation of wild germplasm, a great amount of diversity that might be useful for the generation of new poinsettia cultivars could be lost. The only official Mexican measure for the management and conservation of poinsettia wild germplasm is indirect protection a few wild poinsettia populations are within Mexican parks or reserves. Our results show how geographic proximity does not always predict genetic similarity and underscores the usefulness of mapping the geographic distribution of genetic variation.

Our results highlight populations that are priorities for conservation because of their haplotype diversity, high human footprint values, or haplotypes not protected in parks or reserves (Table 2). Priority should be given to the protection of populations whose disappearance would lead to the loss of unique variation, e.g., the wild population with white bracts (Table 2). Populations near metropolitan areas are generally priorities because they are the most prone to disappear. Such is the case for populations in Morelos, which have very high human footprint scores and are being surrounded by urban growth. It is also important to give priority to populations with historic value, such as the likely ancestral populations from northern Guerrero, where habitats also have been damaged by deforestation and lack protection.

Our fieldwork showed that most extinct poinsettia populations grew in relatively flat, rolling country, as opposed to the steep canyon slopes where the species is usually found. The steepness of most poinsettia localities mean that many populations seem to persist because agriculture or human settlements reach the lips of canyons but leave the slopes sufficiently intact as to permit the survival of some plants. Given the lack of information regarding pollinators and dispersal, the extent to which agriculture and urbanization affect gene flow is unknown. Poinsettia populations may continue to persist in canyons, protected by their inaccessibility. Certainly such canyons could be afforded protection as local parks.

Conclusions— The study of centers of origin is a fundamental step for locating the ancestors of domesticates, understanding

the process of domestication, and for designing breeding and conservation strategies. Recent domesticates have the advantage of extant, relatively unaltered wild populations, documentation regarding the objectives of the domestication, and historical records or at least traditions documenting their spread by humans. We combined three sources of evidence, historical, genetic, and environmental, to identify the ancestors of the cultivars of one the world's most economically important plants, the poinsettia. The confluence of evidence identified a small region of northern Guerrero as the likely region. This information not only provides the foundation for studies of evolution under domestication in poinsettia, but we now have an accurate guide to search for new genetic variation to improve the many shortcomings of the crop. Particularly desirable would be cultivars that tolerate stressful environmental conditions such as cold, drought, and high humidity (Parks and Moyer, 2004; Ecke, 2011), more resistance to pests such as glasshouse whitefly, pathogens such as *Pythium*, *Phytophthora*, and *Botrytis* (Potter and Eames, 1997), or to mechanical damage caused by jostling during production and transportation (Ecke, 2011). Knowledge of its provenance should invigorate breeding, research, and conservation of this iconic plant.

LITERATURE CITED

AKAIKE, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19: 716–723.

ARRIAGA, L., J. M. ESPINOZA-RODRÍGUEZ, C. AGUILAR-ZÚÑIGA, E. MARTÍNEZ-ROMERO, L. GÓMEZ-MENDOZA, AND E. LOA [eds.]. 2000. Regiones prioritarias terrestres de México. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México D.F., México.

BAIG, M., A. BEJA-PEREIRA, R. MOHAMMAD, K. KULKARNI, S. FARAH, AND G. LUIKART. 2005. Phylogeography and origin of Indian domestic cattle. *Current Science* 89: 38–40.

BURGER, J. C., M. A. CHAPMAN, AND J. M. BURKE. 2008. Molecular insights into the evolution of crop plants. *American Journal of Botany* 95: 113–122.

CEUM. 2011. Ley General del Equilibrio Ecológico y Protección al Ambiente. Diario Oficial, México D.F., México.

CLEMENT, M., D. POSADA, AND K. A. CRANDALL. 2000. TCS: A computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657–1659.

DIAMOND, J. 2002. Evolution, consequences and future of plant and animal domestication. *Nature* 418: 700–706.

DIBBLE, C. E., AND A. J. O. ANDERSON. 1963. Florentine Codex, book 11, no. 14, part XII. School of American Research and University of Utah, Santa Fe, New Mexico and Salt Lake City, Utah, USA.

DRISCOLL, C. A., M. MENOTTI-RAYMOND, A. L. ROCA, K. HUPE, W. E. JOHNSON, E. GEFFEN, E. H. HARLEY, ET AL. 2007. The near eastern origin of cat domestication. *Science* 317: 519–529.

ECKE, P. 2011. Poinsettia. Paul Ecke Poinsettias, Encintas, California. USA.

ECKE, P., A. MATKIN, AND D. E. HARTLEY. 1990. The poinsettia manual. Paul Ecke Poinsettias, Encintas, California, USA.

EMSHWILLER, E. 2006. Genetic data and plant domestication. *In* M. A. Zeder, E. Emshwiller, D. G. Bradley, and B. D. Smith [eds.], Documenting domestication: New genetic and archaeological paradigms, 99–122. University of California Press, Berkeley, California, USA.

ERIKSSON, J., G. LARSON, U. GUNNARSSON, B. BED'HOM, M. TIXIER-BOICHARD, L. STRÖMSTEDT, D. WRIGHT, ET AL. 2008. Identification of the *yellow skin* gene reveals a hybrid origin of the domestic chicken. *PLoS Genetics* 4: e1000010.

EXCOFFIER, L., G. LAVAL, AND S. SCHNEIDER. 2005. Arlequin ver. 3.0: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* 1: 47–50.

FARRIS, J. S., M. KÄLLERJÖ, A. G. KLUGE, AND C. BULT. 1994. Testing significance of incongruence. *Cladistics* 10: 315–319.

FERIA ARROYO, T. P., M. E. OLSON, A. GARCÍA-MENDOZA, AND E. SOLANO. 2009. A GIS-based comparison of the Mexican national and IUCN criteria for determining extinction risk. *Conservation Biology* 23: 1156–1166.

FIELDING, A. H., AND J. F. BELL. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49.

FRY, J. 1994. The introduction of the poinsettia at Bartram's Garden. Bartram Broadside, Philadelphia, Pennsylvania, USA.

GASKIN, J. F., AND B. A. SCHAAL. 2002. Hybrid *Tamarix* widespread in U.S. invasion and undetected in native Asia range. *Proceedings of the National Academy of Sciences, USA* 99: 11256–11259.

GOLOBOFF, P. A. 1999. NONA, version 2.0 for Windows. Computer program and documentation distributed by the author, website http://www.cladistics.com [accessed 17 May 2012].

GRAHAM, R. 1836. Description of several new or rare plants which have lately flowered in the neighbourhood of Edinburgh chiefly in the Royal Botanic Garden. *Edinburgh New Philosophical Journal* 20: 412–413.

GUISAN, A., AND N. E. ZIMMERMANN. 2000. Predictive habitat distribution models in ecology. *Ecological Modelling* 135: 147–186.

GUNN, B. F., L. BAUDOUIN, AND K. M. OLSEN. 2011. Independent origins of cultivated coconut (*Cocos nucifera* L.) in the Old World tropics. *PLoS ONE* 6: e21143.

HAMILTON, M. B. 1999. Tour primer for the amplification of chloroplast intergenic regions with intraspecific variation. *Molecular Ecology* 8: 513–525.

HARTER, A. V., K. A. GARDNER, AND D. FALUSH. 2004. Origin of extant domesticated sunflowers in eastern North America. *Nature* 430: 201–205.

HAUDRY, A., A. CENCI, C. RAVEL, T. BATAILLON, D. BRUNEL, C. PONCET, I. HOCHU, ET AL. 2007. Grinding up wheat: A massive loss of nucleotide diversity since domestication. *Molecular Biology and Evolution* 24: 1506–1517.

HERNÁNDEZ, F. 1946. Historia de las plantas de la Nueva España, vol. III, 958–960. Universidad Nacional Autonoma de México, México D.F., México.

HERNÁNDEZ, F. 1959. Obras completas, vol. II and III, 319–320. Universidad Nacional Autonoma de México, México D.F., México.

HIJMANS, R. J., S. E. CAMERON, J. L. PARRA, P. G. JONES, AND A. JARVIS. 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* 25: 1965–1978.

HUELSENBECK, J. P., AND F. RONQUIST. 2001. MrBayes: Bayesian inference of phylogenetictrees. *Bioinformatics* 17: 754–755.

KOCHHAR, S. L. 1998. Economic botany in the tropics. Man Millan India, Daryaganj, New Delhi, India.

KWAK, M., J. A. KAMI, AND P. GEPTS. 2009. The putative Mesoamerican domestication center of *Phaseolus vulgaris* is located in the Lerma-Santiago Basin of Mexico. *Crop Science* 49: 554–563.

LARSON, G., U. ALBARELLA, K. DOBNEY, P. ROWLEY-CONWY, J. SCHIBLER, AND A. TRESSET, J.-D. VIGNE, ET AL. 2007. Ancient DNA, pig domestication, and the spread of the Neolithic into Europe. *Proceedings of the National Academy of Sciences, USA* 104: 15276–15281.

LARSON, G., K. DOBNEY, U. ALBARELLA, M. FANG, E. MATISOO-SMITH, J. ROBINS, S. LOWDEN, ET AL. 2005. Worldwide phylogeography of wild boar reveals multiple centers of pig domestication. *Science* 307: 1618–1621.

MARSHALL, C. J., AND J. K. LIEBHERR. 2000. Cladistic biogeography of the Mexican transition zone. *Journal of Biogeography* 27: 203–216.

MAS, J. F., A. VELÁZQUEZ, J. R. DÍAZ-GALLEGOS, R. MAYORGA-SAUCEDO, C. ALCÁNTARA, G. BOCCO, R. CASTRO, ET AL. 2004. Assessing land use/cover changes: A nationwide multidate spatial database for Mexico. *International Journal of Applied Earth Observation and Geoinformation* 5: 249–261.

MAYFIELD, M. H. 1997. A systematic treatment of *Euphorbia* subgenus *Poinsettia* (Euphobiaceae). Ph.D. dissertation, University of Texas, Austin, Texas, USA.

MCCORMACK, J. E., A. T. PETERSON, E. BONACCORSO, AND T. B. SMITH. 2008. Speciation in the highlands of Mexico: Genetic and phenotypic divergence in the Mexican jay (*Apheloma ultramarina*). *Molecular Ecology* 17: 2505–2521.

MCGINTY, B. 1980. The poinsettia. *Early American Life* 11: 38–39, 72–74.

MILLER, A. J., AND J. H. KNOUFT. 2006. GIS-based characterization of the geographic distributions of wild and cultivated populations of the Mesoamerican fruit tree *Spondias purpurea* (Anacardiaceae). *American Journal of Botany* 93: 1757–1767.

MILLER, A. J., AND B. A. SCHAAL. 2005. Domestication of a Mesoamerican cultivated fruit tree, *Spondias purpurea. Proceedings of the National Academy of Sciences, USA* 102: 12801–12806.

MOON, M. H. 1956. A short history of the poinsettia. *Baileya* 4: 176–181.

MORRELL, P. L., AND M. T. CLEGG. 2007. Genetic evidence for a second domestication of barley (*Hordeum vulgare*) east of the Fertile Crescent. *Proceedings of the National Academy of Sciences, USA* 104: 3289–3294.

NAVARRO, J. 1992. Historial natural o jardín americano (manuscrito de 1801). Universidad Nacional Autónoma de México, Instituto Mexicano del Seguro Social, and Instituto de Seguridad y Servicios Sociales de los Trabajadores del Estado, México D.F., México.

NIXON, K. C. 2002. WinClada version 1.00.08 for Windows. Computer program and documentation distributed by the author, website http://www.cladistics.com [accessed 17 May 2012].

OLSEN, K. M., AND B. A. SCHAAL. 1999. Evidence on the origin of cassava: Phylogeography of *Manihot esculenta. Proceedings of the National Academy of Sciences, USA* 96: 5586–5591.

OUTRAM, A. K., N. A. STEAR, R. BENDREY, S. OLSEN, A. KASPAROV, V. ZALBERT, N. THORPE, AND R. P. EVERSHED. 2009. The earliest horse harnessing and milking. *Science* 323: 1332–1335.

PARKS, E. J., AND J. W. MOYER. 2004. Evaluation of AFLP in poinsettia: Polymorphism selection, analysis, and cultivar identification. *Journal of the American Society for Horticultural Science* 129: 863–869.

PARTHASARATHY, N. 1948. Origin of noble sugar-canes (*Saccharum officinarum*). *Nature* 161: 608.

PHILLIPS, S. J. 2008. Transferability, sample selection bias and background data in presence-only modelling: A response to Peterson et al. (2007). *Ecography* 31: 272–278.

PHILLIPS, S. J., R. P. ANDERSON, AND R. E. SCHAPIRE. 2006. Maximum entropy modeling of species geographic distribution. *Ecological Modelling* 190: 231–259.

PHILLIPS, S. J., M. DUDÍK, AND R. E. SCHAPIRE. 2004. A maximum entropy approach to species distribution modeling. *In* R. Greiner and D. Schuurmans [eds.], Machine learning: Proceedings of the Twenty-first Century International Conference on Machine Learning, Banff, 655–662. ACM Press, Banff, Canada.

POTTER, R., AND A. EAMES. 1997. Poinsettia essentials. Royal Botanical Garden, Edinburgh, UK.

POSADA, D., AND K. A. CRANDALL. 1998. ModelTest: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

RAFINESQUE, C. S. 1833. *Pleuradena coccinea*. *Atlantic Journal* 1: 182.

RAMBAUT, A. 2002. SE-AL: Sequence Alignment Editor, version 2.0a11. Computer program and documentation distributed by the author, website: http://tree.bio.ed.ac.uk/software/seal [accessed 23 February 2008].

RONALDSON, J. 1828. Letter to J. R. Poinsett (Nov. 6). Poinsett papers, vol. 5, folder 9, no. 83. Historical Society of Pennsylvania, Philadelphia, Pennsylvania, USA.

SAMBROOK, J., E. F. FRITSCH, AND T. MANIATIS. 1989. Molecular cloning: A laboratory manual, 2nd ed. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, New York, USA.

SANDERSON, E. W., M. JAITEH, M. A. LEVY, K. H. REDFORD, A. V. WANNEBO, AND G. WOOLMER. 2002. The human footprint and the last of the wild. *BioScience* 52: 891–904.

SANG, T., D. J. CRAWFORD, AND T. F. STUESSY. 1997. Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paenoia* (Paeoniaceae). *American Journal of Botany* 84: 1120–1136.

SAY, T. 1828. List of Mexican seeds, "Sent to Mr. Carr by Mr. Moffett, letter July 23rd., 1828." Say Papers, coll. 455. Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania, USA.

SMALLEY, J., AND M. BLAKE. 2003. Sweet beginnings: Stalk sugar and the domestication of maize. *Current Anthropology* 44: 675–703.

SOLANO, E., AND T. P. FERIA. 2007. Ecological niche modeling and geographic distribution of the genus *Polianthes* L. (Agavaceae) in Mexico: Using niche modeling to improve assessments of risk status. *Biodiversity and Conservation* 16: 1885–1900.

SPOONER, D. M., K. MCLEAN, G. RAMSAY, R. WAUGH, AND G. BRYAN. 2005. A single domestication for potato based on multilocus amplified fragment length polymorphism genotyping. *Proceedings of the National Academy of Sciences, USA* 102: 14694–14699.

STEINMANN, V. W., AND J. M. PORTER. 2002. Phylogenetic relationships in *Euphorbieae* (Euphorbiaceae) based on ITS and *ndh*F sequence data. *Annals of the Missouri Botanical Garden* 89: 453–490.

STRAND, A. E., J. LEEBENS-MACK, AND B. G. MILLIGAN. 1997. Nuclear DNA-based markers for plant evolutionary biology. *Molecular Ecology* 6: 113–118.

TAYLOR, J. M., R. G. LOPEZ, C. J. CURREY, AND J. JANICK. 2011. The poinsettia: History and transformation. *Chronica Horticulturae* 51: 23–28.

TEMPLETON, A. R., K. A. CRANDALL, AND C. F. SING. 1992. A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data III. Cladogram estimation. *Genetics* 132: 619–633.

USDA AND NASS. 2011. Floriculture crops 2010 summary. U. S. Government Printing Office, Washington, D.C., USA.

VILÀ, C., P. SAVOLAINEN, J. E. MALDONADO, I. R. AMORIM, J. E. RICE, R. L. HONEYCUTT, K. A. CRANDALL, ET AL. 1997. Multiple and ancient origins of the domestic dog. *Science* 276: 1687–1689.

XIA, Q., Y. GUO, Z. ZHANG, D. LI, Z. XUAN, Z. LI, F. DAI, ET AL. 2009. Complete resequencing of 40 genomes reveals domestication events and genes in silkworm (*Bombyx*). *Science* 326: 433–436.

ZEDER, M. A., E. EMSHWILLER, B. D. SMITH, AND D. G. BRADLEY. 2006. Documenting domestication: The intersection of genetics and archaeology. *Trends in Genetics* 22: 139–155.

ZIMMERMANN, N. F. A., C. M. RITZ, AND F. H. HELLWING. 2010. Further support for the phylogenetic relationships within *Euphorbia* L. (Euphorbiaceae) from nrITS and *trn*L-*trn*F IGS sequence data. *Plant Systematics and Evolution* 286: 39–58.

ZOHARY, D. 2004. Unconscious selection and the evolution of domesticated plants. *Economic Botany* 58: 5–10.