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RESEARCH ARTICLE

Molecular evidence for repeated recruitment of wild Christmas poinsettia (*Euphorbia pulcherrima*) into traditional horticulture in Mexico

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Abstract One of Mexico's most emblematic and economically important plants is the poinsettia (*Euphorbia pulcherrima*). After nearly 200 years of poinsettia cultivation outside Mexico, more than 300 varieties of many different sizes, shapes and colors have been generated. However, studies on the management of or the evolutionary processes through which the changes present in cultivars have been generated, starting from wild plants, have not been carried out. In the present work, we tested the hypothesis that poinsettia plants living in human settlements represent transplanted wild plants. To test this hypothesis, we analyzed the genetic diversity and kin relationships of 58 poinsettia plants from 25 wild populations, 25 garden plants and 8 Mexican and foreign cultivars. Two non-coding intergenic chloroplast markers, *trnG-trnS* and *psbA-trnH*, were utilized to obtain the diversity indices and genealogies. The results support the transplanting of poinsettias hypothesis because garden plants share the same genetic variant as the wild populations and, in most cases, that of the closest wild populations. Some garden poinsettias have simple inflorescences, like the wild plants. The garden plants have a genetic diversity that is higher than in cultivars and that is shared with nearby wild populations. Additionally, some homeowners indicated that their plants were obtained from nearby hills. The transplanting of wild poinsettia plants to human settlements could have been one of the first steps in the domestication process of *E. pulcherrima*. Also, new genetic variants were found; one of these could be *Euphorbia fastuosa*, an invalid name for *E. pulcherrima* proposed by Sessé and Mociño between 1787 and 1803.

Keywords Domestication · *Euphorbia pulcherrima* · Genealogies · Management · Poinsettia · Wild relatives

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Introduction

Mexico is part of Mesoamerica, one of the word´s main centers of plant domestication (Vavilov 1951). Among Mexico´s most emblematic plants is the poinsettia (*Euphorbia pulcherrima* Willd. ex

Klotzsch). It is a floral symbol of Christmas, with sales of over 100 million dollars in the US alone (USDA 2016). Currently, there are more than 300 cultivars of various sizes and colors. The wild populations of poinsettias are found along the Pacific coast, from Sinaloa, Mexico, to Guatemala, and extend into central Mexico from Guerrero to Morelos (Trejo et al. 2012). Despite the poinsettia's great biocultural and economic importance, it remains, from various biological, ecological and evolutionary aspects, a little-studied plant. For example, despite the fact that cultivars have notable differences in size and color compared to wild plants (Fig. 1), there are no studies regarding its traditional management or to what degree it has been altered by domestication.

Domestication is a human-driven interaction between organisms and humans in which the domesticated organism can undergo morphological and genetic changes and adaptations with respect to its wild relatives (Pickersgill 2007). Management consists of patterns of human action in the interactions with organisms, such as enhancing certain wild plants by increasing their survival rate by eliminating other plants which compete for light or nutrients and transplants, in which humans take cuttings and entire wild plants into cultivation. This management is part of the change process in plants that can lead to their domestication (Casas et al. 1997).

Previous studies have demarcated the potential distribution of wild poinsettias and characterized their genetic diversity (Trejo et al. 2012). These studies have shown that the main source of germplasm for the commercial cultivars in the United States is located in northern Guerrero, Mexico (Trejo et al. 2012). However, since pre-Columbian times to the present day, various poinsettia plants have been reported in human settlements throughout its natural range (Trejo-Hernández et al. 2015). Wild plants differ from commercial cultivars in stalk length, internode length and leaf area (Trejo et al. 2018). They have simple inflorescences, i.e., with a single row of bracts, whereas commercial cultivars present both double (with multiple rows) and simple inflorescences. Plants with double inflorescences have not been observed in wild populations. Some plants with simple inflorescences, found in human settlements, could be wild plants transplanted from geographically close wild populations (Trejo-Hernández et al. 2015). Transplantation could be an initial step in the process of generating traditional cultivars and in the domestication of the poinsettia. In the present study, we tested the hypothesis that poinsettia plants living in human settlements are transplanted wild plants (Trejo-Hernández et al. 2015), for which we utilize intergenic chloroplast sequence molecular markers to recognize the kin relationships (network haplotype, genealogy) between plants in human settlements and wild populations of *E. pulcherrima*.

Materials and methods

Collecting

Throughout the natural distribution of *E. pulcherrima* (Trejo et al. 2012), we collected, between 2007 and 2016, 25 plants in human settlements such as gardens, backyards plots, parks, cemeteries and road medians (Table 1). Additionally, three new populations were collected with respect to Trejo et al. 2012 and Trejo-Hernández et al. 2015. In Fig. 1, we present examples of wild plants, plants in human settlements (garden poinsettias), and cultivated plants that were analyzed in this work. At each plant collecting site in human settlements, the origin of the plants was inquired about.

Sequencing

Trejo et al. (2012) protocols were used to extract DNA, amplify the fragments by means of PCR and sequence two non-coding intergenic markers: *trnG*$^{(UCC)}$–*trnS*$^{(GCU)}$ (Hamilton 1999) and *psbA-trnH* (Sang et al. 1997).

Data analysis

Data matrix

A general matrix was generated with Trejo et al. (2012, Trejo-Hernández et al. 2015) data and the new data presented in this work: the garden plants and three new wild populations. We used the outgroups *E. cornastra* Dressler and *E. heterophylla* L. based on the phylogeny of the genus by Steinmann and Porter (2002) and Zimmermann et al. (2010). Regarding *E. pulcherrima*, we analyzed a total of 58 individuals: 25 from wild populations, 6 cultivars from the US, 2

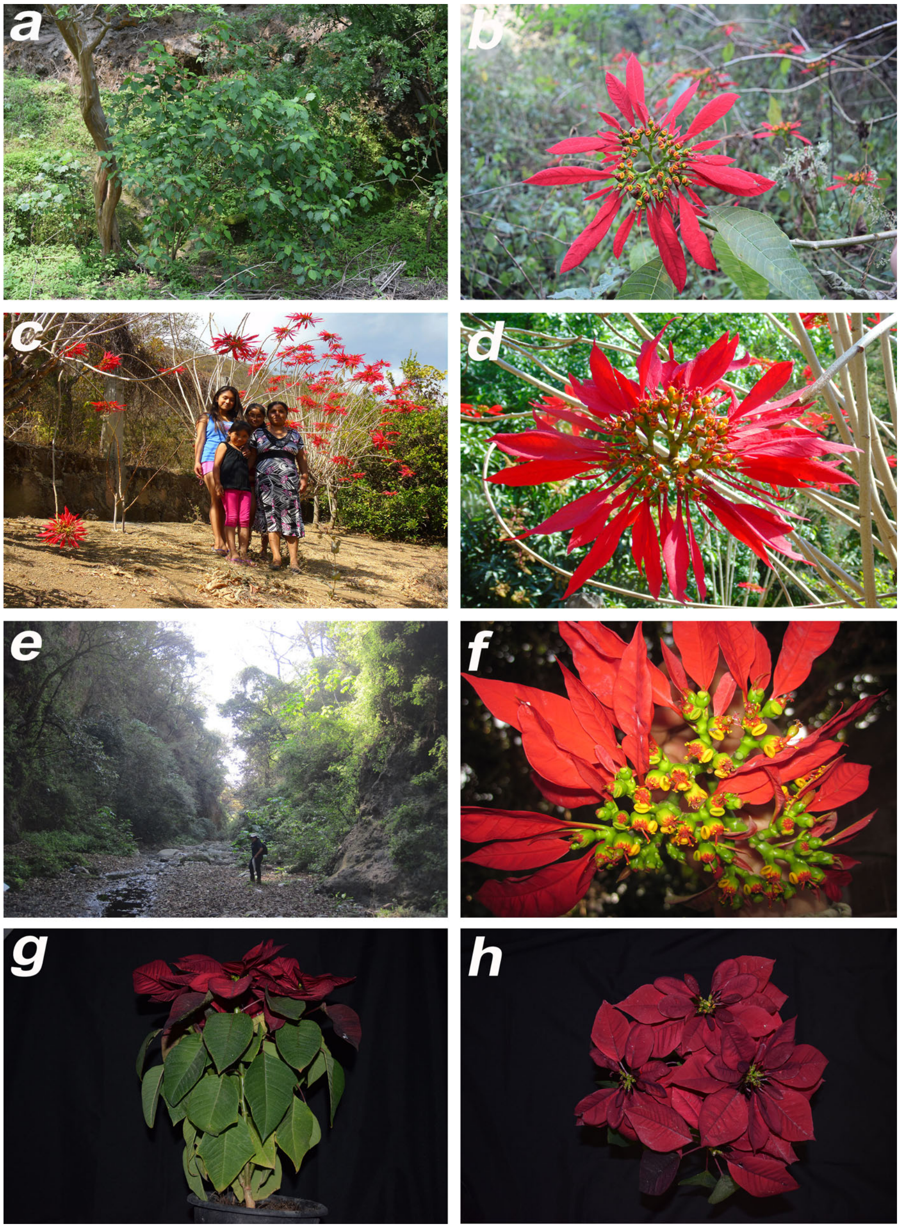

Fig. 1 Poinsettia plants (*Euphorbia pulcherrima*). **a** poinsettia plant from Amatlán de Quetzalcoatl, Morelos; **b** inflorescence of the plant in (**a**), **c** poinsettia plant in the garden of a house in Atzalán, Guerrero, **d** inflorescence of the plant in (**b**), **e** ravines in Xochitlán, Morelos (population possibly collected by Sessé and Mociño between 1787 and 1805), **f** inflorescence of the plant in (**e**), **g** Maroon Prestige cultivar plant, **h** inflorescence of the plant in (**g**)

cultivars from Mexico and 25 plants from human settlements or gardens.

Analysis of genetic diversity

We calculated various summary statistics that describe the levels of genetic diversity such as number of haplotypes (h), haplotype diversity ($Hd \pm$ SD); nucleotide diversity (π); average number of nucleotide differences (k); number of polymorphic, segregating sites (S); parsimony-informative sites (P) and theta (per site) from S (theta-W). The indices were calculated for each group of wild plants, garden plants, and

Table 1 *Euphorbia pulcherrima*. Analyzed plants and information on origin, genetic variant, inflorescence type and reference

Species	Collection no.	Category	Source/cultivar	H_{cp}	Inflorescence	*psbA-trnH*	*trnG-trnS*	References
E. pulcherrima	1071	Wild	Concordia, Sinaloa	1	Simple	HM155953	HM156016	Trejo et al. (2012)
E. pulcherrima	1073	Wild	Compostela, Nayarit	1	Simple	HM155955	HM156018	Trejo et al. (2012)
E. pulcherrima	**1065-II**	**Garden**	**El Palmito, Sinaloa**	**1**	**Simple**	**MH521193**	**MH521219**	**En este trabajo**
E. pulcherrima	62	Wild	La Calera, Jalisco	2	Simple	HM155975	HM156038	Trejo et al. (2012)
E. pulcherrima	1076	Wild	Talpa de Allende, Jalisco	2	Simple	HM155948	HM156011	Trejo et al., 2012
E. pulcherrima	1071 A	Wild	Concordia, Sinaloa	2	Simple	HM155950	HM156013	Trejo et al. (2012)
E. pulcherrima	1085	Wild	Aquila, Michoacán	3	Simple	HM155957	HM156020	Trejo et al. (2012)
E. pulcherrima	1086	Wild	Aquila, Michoacán	4	Simple	HM155959	HM156022	Trejo et al. (2012)
E. pulcherrima	8	Wild	San Andrés, Guerrero	5	Simple	HM155925	HM155988	Trejo et al. (2012)
E. pulcherrima	11	Wild	Petatlán, Guerrero	5	Simple	HM155928	HM155991	Trejo et al. (2012)
E. pulcherrima	114	Wild	Barrancas de la Peña, Guerrero	5	Simple	HM155930	HM155993	Trejo et al. (2012)
E. pulcherrima	**71**	**Garden**	**Coyoacán, CDMX**	**5**	**Simple**	**KF809827**	**KF809848**	**Trejo-Hernández et al.** (2015)
E. pulcherrima	**132**	**Garden**	**Álvaro Obregón, CDMX**	**5**	**Doble**	**KF809826**	**KF809849**	**Trejo-Hernández et al.** (2015)
E. pulcherrima	**65**	**Garden**	**Taxco, Guerrero**	**5**	**Simple**	**MH521196**	**MH521222**	**In this work**
E. pulcherrima	**113**	**Garden**	**Teloloapán, Guerrero**	**5**	**Simple**	**MH521198**	**MH521224**	**In this work**
E. pulcherrima	**31**	**Garden**	**Amatlán, Morelos**	**5**	**Simple**	**MH521195**	**MH521221**	**In this work**
E. pulcherrima	**89**	**Garden**	**Tepoztlán, Morelos**	**5**	**Doble**	**MH521197**	**MH521223**	**In this work**
E. pulcherrima	73	Cultivar	Sub-Jibi	5	Doble	HM155918	HM155981	Trejo et al. (2012)
E. pulcherrima	74	Cultivar	Freedom Red	5	Doble	HM155916	HM155979	Trejo et al. (2012)
E. pulcherrima	76	Cultivar	Red Glitter	5	Doble	HM155921	HM155984	Trejo et al. (2012)
E. pulcherrima	44	Cultivar	Prestige Red	5	Doble	KF809829	KF809847	Trejo et al. (2012)
E. pulcherrima	64	Wild	Taxco, Guerrero	6	Simple	HM155935	HM155998	Trejo et al. (2012)
E. pulcherrima	68	Wild	Texcal, Morelos	6	Simple	HM155933	HM155996	Trejo et al. (2012)
E. pulcherrima	107	Wild	Tepoztlán, Morelos	6	Simple	HM155938	HM156001	Trejo et al. (2012)
E. pulcherrima	115	Wild	Taxco, Guerrero	6	Simple	HM155940	HM1556003	Trejo et al. (2012)
E. pulcherrima	1257	Wild	Tepoztlán, Morelos	6	Simple	JQ666170	JQ666172	Trejo et al. (2012)
E. pulcherrima	**165**	**Garden**	**Milpa Alta, CDMX**	**7**	**Simple**	**KF809804**	**KF809837**	**Trejo-Hernández et al.** (2015)
E. pulcherrima	**160**	**Garden**	**M. Contreras, CDMX**	**7**	**Doble**	**KF809812**	**KF809843**	**Trejo-Hernández et al.** (2015)
E. pulcherrima	**67**	**Garden**	**Taxco, Guerrero**	**7**	**Simple**	**MH521201**	**MH521227**	**In this work**
E. pulcherrima	**25**	**Garden**	**Amatlán, Morelos**	**7**	**Simple**	**MH521200**	**MH521226**	**In this work**
E. pulcherrima	**22**	**Garden**	**Tepoztlán, Morelos**	**7**	**Simple**	**MH521199**	**MH521225**	**In this work**
E. pulcherrima	**88**	**Garden**	**UAEM, Morelos**	**7**	**Simple**	**MH521202**	**MH521228**	**In this work**
E. pulcherrima	**370**	**Garden**	**Santa Ana, Tlaxcala**	**7**	**Simple**	**MH521203**	**MH521229**	**In this work**

Table 1 continued

Species	Collection no.	Category	Source/cultivar	H_{cp}	Inflorescence	*psbA-trnH*	*trnG-trnS*	References
E. pulcherrima	118	Cultivar	Valenciana	7	Doble	HM155943	HM156006	Trejo et al. (2012)
E. pulcherrima	52	Cultivar	Rehilete	7	Doble	HM155944	HM156007	Trejo et al. (2012)
E. pulcherrima	76	Cultivar	Marble Star	7	Doble	HM155945	HM156008	Trejo et al. (2012)
E. pulcherrima	44	Cultivar	Monet	7	Doble	HM155946	HM156009	Trejo et al. (2012)
E. pulcherrima	104	Wild	Tierra Colorada, Guerrero	8	Simple	HM155970	HM156033	Trejo et al. (2012)
E. pulcherrima	60	Wild	Palo Blanco, Guerrero	9	Simple	HM155967	HM156030	Trejo et al. (2012)
E. pulcherrima	18	Wild	Concordia, Oaxaca	10	Simple	HM155973	HM156036	Trejo et al. (2012)
E. pulcherrima	1106	Wild	Ocozocuautla, Chiapas	11	Simple	HM155965	HM156028	Trejo et al. (2012)
E. pulcherrima	1108	Wild	Río Tablón, Chiapas	11	Simple	HM155963	HM156026	Trejo et al. (2012)
E. pulcherrima	56	Wild	Sacatepéquez, Guatemala	12	Simple	HM155961	HM156024	Trejo et al. (2012)
E. pulcherrima	**373 B**	**Wild**	**Landa I, Guerrero**	**13**	**Simple**	**MH521207**	**MH521233**	**In this work**
E. pulcherrima	**373 R**	**Wild**	**Landa I, Guerrero**	**13**	**Simple**	**MH521208**	**MH521234**	**In this work**
E. pulcherrima	**380**	**Wild**	**Xochitlán, Morelos**	**13**	**Simple**	**MH521211**	**MH521237**	**In this work**
E. pulcherrima	**384**	**Wild**	**Tepoztlán, Morelos**	**13**	**Simple**	**MH521214**	**MH521240**	**In this work**
E. pulcherrima	**375**	**Garden**	**Atzalán, Guerrero**	**13**	**Doble**	**MH521209**	**MH521235**	**In this work**
E. pulcherrima	**372**	**Garden**	**Landa IV, Guerrero**	**13**	**doble**	**MH521206**	**MH521232**	**In this work**
E. pulcherrima	**82**		**Tierra Colorada, Guerrero**	**13**	**Simple**	**MH521204**	**MH521230**	**In this work**
E. pulcherrima	**872 A**	**Garden**	**Malinalco, Estado de México**	**13**	**Simple**	**MH521216**	**MH521243**	**In this work**
E. pulcherrima	**872 C**	**Garden**	**Malinalco, Estado de México**	**13**	**Simple**	**MH521217**	**MH521242**	**In this work**
E. pulcherrima	**385**	**Garden**	**Tepoztlán, Morelos**	**13**	**Simple**	**MH521215**	**MH521241**	**In this work**
E. pulcherrima	**379**	**Garden**	**Xochitlán, Morelos**	**13**	**Doble**	**MH521210**	**MH521236**	**In this work**
E. pulcherrima	**381**	**Garden**	**Xochitlán, Morelos**	**13**	**Simple**	**MH521212**	**MH521238**	**In this work**
E. pulcherrima	**382**	**Garden**	**Xochitlán, Morelos**	**13**	**Simple**	**MH521213**	**MH521239**	**In this work**
E. pulcherrima	**371**	**Garden**	**Tlaxcala, Tlaxcala**	**13**	**Simple**	**MH521205**	**MH521231**	**In this work**
E. pulcherrima	**330**	**Garden**	**Concordia, Oaxaca**	**14**	**Simple**	**MH521218**	**MH521244**	**In this work**
E. cornastra	61	Wild	Tlacotepec, Guerrero	15	Simple	HM155978	HM156041	Trejo et al. (2012)
E. heterophylla	63	Wild	La Calera, Jalisco	16	Simple	HM155977	HM156064	Trejo et al. (2012)

The bold indicates new samples obtained in this work cultivars using DnaSP v.5.10.01 (Librado and Rozas 2009).

Kin relationships

To describe kin relationships, Bayesian trees and haplotype networks were used. For the Bayesian analyses, the evolutionary model that best describes the mutation rate according to the Akaike criterion in JModelTest 2.1.10 (Darriba et al. 2012) was selected. The two chloroplast markers were analyzed jointly in MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001) with 4 Markov chains for 4 million generations and at a temperature of 0.04. Finally, 25% of the topologies were discarded as burn-in. For the haplotypes network, a parsimonious analysis with TCS (Clement et al. 2000) was carried out; the gaps were taken as missing data and the networks were built with a 95% connectivity limit.

Results

Genetic diversity

By linking together the *trnG*$^{(UCC)}$-*trnS*$^{(GSU)}$ and *psbA-trnH* primers, a 60 sequence matrix with a length of 1587 bp was obtained. The wild populations had the highest genetic diversity indices while the cultivars had the lowest. Garden plants had intermediate diversity values (Table 2).

Regarding previous studies, two new genetic variants, or haplotypes, were found. One variant was observed in newly collected wild populations in Guerrero and Morelos and the second in a garden plant in Oaxaca.

Kin relationships

In the haplotype network as well as in the posterior probability tree, we observed that wild populations are genetically closer to one another given closer geographical distance. The populations, however, didn't show evidence of isolation by distance. In 60% of the states where garden plants were analyzed (Morelos, Guerrero and Sinaloa), the garden plant haplotype was the same as that of the plants from the closest wild population. Some plants presented simple inflorescences (with a single row of bracts). Asked about the origin of their plants, most people reported being unaware of it; only in Guerrero and in Morelos was it indicated that the plants were brought from the hills and, in Mexico City, two persons said that their plants came from their houses in Guerrero and Morelos.

We also observed that the cultivars had two haplotypes: haplotype 5, which characterizes the United States cultivars (whose germoplasm source is in northern Guerrero), and haplotype 7, which is found in commercial poinsettia cultivars developed in Mexico and whose wild germplasm source is still unknown (Trejo et al. 2012; Trejo-Hernández et al. 2015). The three new populations that were analyzed represent a new haplotype (13) that is found in wild populations of Morelos and Guerrero and garden plants of Guerrero and central Mexico (Table 1). These populations are geographically close to other populations from northern Guerrero and Morelos (Figs. 2, 3).

Discussion

High genetic diversity and different origins of garden poinsettias

In various studies it has been observed that domesticated plants are the result of bottlenecks with respect

Table 2 Summary statistics that describe the genetic diversity between the groups of wild plants, garden plants and cultivars of *E. pulcherrima*

Category	*h*	Hd ± SD	π	*k*	*S*	*P*	theta-W
Wild	12	0.920 ± 0.029	0.00788	8.923	42	29	0.00982
Garden	5	0.730 ± 0.048	0.00285	3.087	18	5	0.00440
Cultivar	2	0.571 ± 0.094	0.00144	1.714	3	3	0.00097

h number of haplotypes, *Hd* haplotype diversity, π nucleotide diversity, *k* average number of nucleotide differences, *S* number of polymorphic (segregating) sites, *P* parsimony informative sites, *theta-W* theta (per site) from *S*

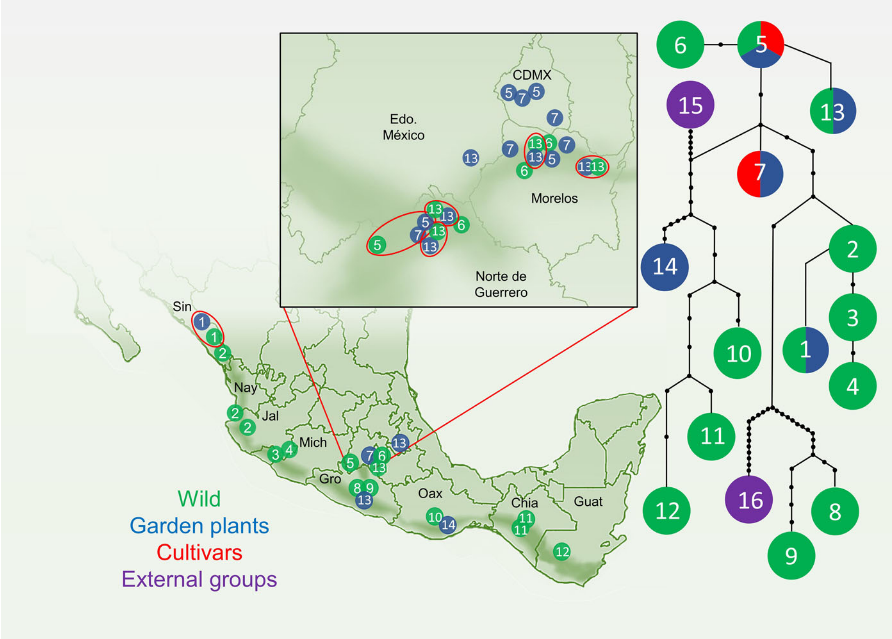

Fig. 2 Haplotypes throughout the distribution of *E. pulcherrima* and haplotype network. The green circles represent wild populations; the blue circles, plants in human settlements or "garden plants" and red circles, cultivars. The red ellipses show the sites in which the garden plants present the same haplotype as the closest wild population

to wild populations. Thus, domesticated plants are often a very small subsample of the genetic diversity of their wild relatives (Pickersgill 2007; Parker et al. 2010). Of the 14 chloroplast genetic variants, or haplotypes, found thus far in the poinsettia, only two (haplotypes 5 and 7) are found in cultivated plants. The genetic diversity in cultivars is only a small fraction of the total diversity of the wild populations of *E. pulcherrima*. A greater diversity was found among garden poinsettias than in cultivars (five haplotypes) and part of this variability is shared with wild plants (haplotypes 1, 5 and 13).

Based on kin relationships, we can state that garden poinsettias can be foreign patented cultivars, Mexican cultivars, or from wild populations. In the gardens of central Mexico, more foreign and Mexican cultivars were found. Mexican cultivar haplotype 7 has not yet been found in a wild population; we found this variant in northern Guerrero, Morelos and Mexico City.

Evidence of transplantation in poinsettias

In the present work, the hypothesis of transplantation of wild poinsettia plants to human settlements is supported because in the states of Sinaloa, Guerrero and Morelos, garden plants present the same haplotype or genetic variant as the closest wild population, and they share strong kin relationships. Some garden plant owners indicated that their plants were obtained from nearby hills. The garden plants have the same appearance as the wild ones, as exemplified by their simple inflorescences. In previous studies, we have observed that wild populations do not present double inflorescences (Trejo et al. 2012, Trejo-Hernández et al. 2015, 2018) and that double inflorescences have been linked to cultivars since prehispanic times (Trejo-Hernández et al. 2015). In 2018, we reported differences in stalk length, intermodal length and leaf area between wild poinsettia plants and commercial cultivars (Trejo et al. 2018). It is possible that these differences may also be present in wild looking garden plants. It is also possible that garden plants show greater genetic diversity than cultivars due to the presence of wild plants in the gardens.

On the other hand, it's conceivable that wild plants could be in human settlements due to other causes; for example, the plants from wild populations that survived the substitution of their habitat for, mostly, urban constructions. However, the plants that were analyzed in this work were collected in house gardens that are not located in areas where wild plants grow, such as ravines. Another scenario could be plants induced in the garden by the sowing of seeds from wild plants.

The use of chloroplast markers has enabled us to know that wild poinsettia populations exhibit a strong

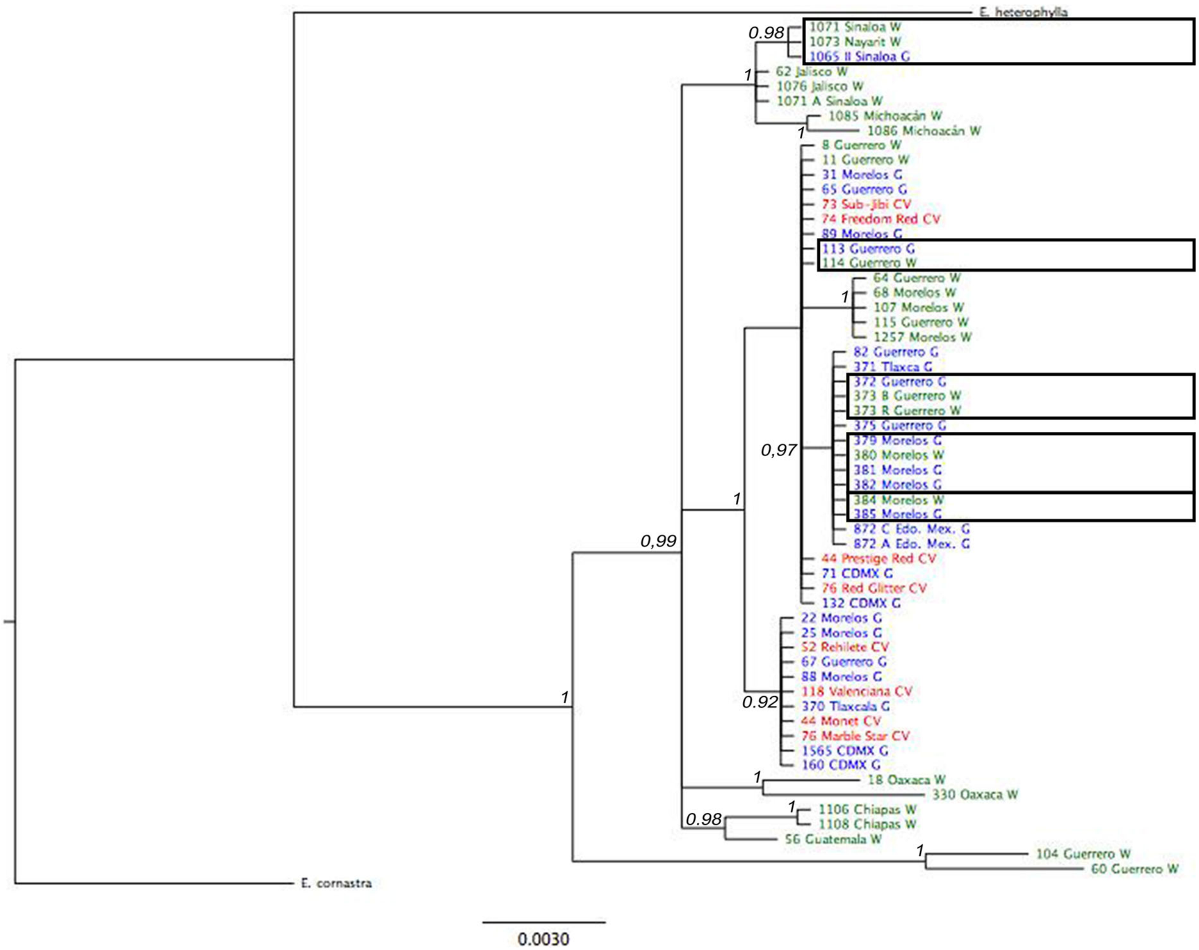

Fig. 3 50% majority-rule consensus cladogram from Bayesian analysis based on chloroplast fragments *psbA-trnH* and *trnG-trnS* (1587 bp; TPMluf + G). The posterior probabilities are shown on the branches. At the tip of each branch, the number and state where collection took place is shown. Wild plants are represented with a green "W"; garden plants with a blue "G" and cultivars with their names in red. *E. cornastra* and *E. heterophylla* are the outgroups. The rectangles show the garden plants present the same haplotype as the closest wild population

population structure (Trejo et al. 2012); in most cases the wild populations present different haplotypes as geographic distance between them increases. This allows for a suitable model to relate cultivars with wild populations. Chloroplast is maternally inherited, therefore it tells only one half of the evolutionary history of the species. The complete history could be known with nuclear markers (Avise 2004). However, Trejo et al. (2012) utilized nuclear markers, but these didn't show resolution, though more research can be done in that direction.

Re-encounter of Sessé and Mociño's poinsettia (*Euphorbia fastuosa* Sessé & Moc.)

Charles III, king of Spain, sent commissioned naturalists to explore the natural riches of his dominions in the Americas. In Mexico, this exploration was named the Royal Botanical Expedition to New Spain and was led by Martín Sessé and José Mariano Mociño between 1787 and 1803 (Mociño 2010). One of the plants described by Sessé and Mociño was the poinsettia, to which the name *Euphorbia fastuosa* was given. Unfortunately, the description of this plant wasn't published until 1888 (Mociño 2010, Lack 2011), after the valid name *Euphorbia pulcherrima* was accepted due to the work of Klotzsch (1834) (Lack 2011).

The only clue to the plants described by Sessé and Mociño is its locality in Xochitlán, state of Morelos, Mexico (Mociño 2010). After 200 years, we went to the ravines of Xochitlán to search for wild *E. pulcherrima* plants. These plants could be *Euphorbia fastuosa* and they present a new haplotype (13), which is distributed in Morelos and in Guerrero.

Toward poinsettia domestication studies

After nearly 200 years of poinsettia cultivation outside Mexico—and at least 500 years in central Mexico—for lack of research there are still many basic open questions regarding the degree to which the poinsettia has been altered under domestication. This work posits that, in the poinsettia selection and domestication process, the management known as transplantation is one of the first events in the domestication of the poinsettia.

To fill some of the most outstanding gaps in knowledge regarding the domestication of poinsettia, it will be necessary to increase the sampling of wild populations and cultivated plants, with special emphasis in the search of haplotype 7 wild populations (currently only known from cultivars developed in Mexico) in central Mexico. Also, morphological and genetic studies that demonstrate genetic changes and adaptations in *E. pulcherrima* resulting from human-driven selection pressures must be carried out. Lastly, we aim to do interdisciplinary studies that allow for a greater integration between molecular ecology and ethnobotanics.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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