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Interdisciplinary insights into the cultural and chronological context of chili pepper (*Capsicum annuum* var. *annuum* L.) domestication in Mexico

Katherine L. Chiou[a,1], Andrés Lira-Noriega[b], Emiliano Gallaga[c], Christine A. Hastorf[d], and Araceli Aguilar-Meléndez[e,1]

Affiliations are included on p. 10.

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This study investigates the temporal and spatial factors driving the domestication of *Capsicum annuum* var. *annuum* L. in Mexico. This species exhibits the greatest morphological diversity in fruit among *Capsicum* species—a characteristic that is even more pronounced in contemporary landraces cultivated by indigenous communities. Despite the chili pepper's integral role in regional culinary traditions, its domestication history in this region remains poorly understood, often subject to scholarly interpretations that marginalize or oversimplify archaeological evidence. To address this gap, our interdisciplinary team of archaeologists, botanists, and ecologists combine modern and archaeological *Capsicum* seed data, diachronic archaeological site locations, and ecological niche modeling to identify potential regions where early human populations and the closest wild ancestors may have coexisted. Our results show spatial correlations between early *Capsicum* distribution and archaeological site prevalence, suggesting that the beginning of the domestication process occurred in ecologically suitable areas for both wild *Capsicum* and human settlement. These findings challenge previous hypotheses regarding highland/dry cave domestication regions, as our data indicate that lowland regions—specifically the Yucatán Peninsula and southern coastal Guerrero—were more conducive to early encounters between wild *Capsicum* and humans. We propose a geographically diffuse and protracted model of chili pepper domestication—driven by a ruderal pathway—which involved at least two asynchronous events across Mexico.

chili pepper origins | ecological niche modeling | paleoethnobotany | plant domestication | Mesoamerican archaeology

Significance

This study weaves together multiple lines of evidence from the Mexican region to address the early domestication trajectory of *Capsicum annuum* var. *annuum* L. The datasets encompass an extensive ethnobotanical collection of modern seeds of *Capsicum* species and cultivars, temporally resolved ecological niche models spanning 20,000 BP to present, morphometric analyses of over a hundred archaeological *Capsicum* seeds for species identification, and spatial distributions of registered archaeological sites in Mexico. This integrative approach enables a more nuanced delineation of *C. annuum*'s domestication locales. Our findings reveal potential origins in southern Mexico, thereby revising the geographic scope of *C. annuum*'s domestication narrative.

Chili peppers (*Capsicum* spp.) are one of the rich and varied crop genetic resources of the Americas. The independent domestication of five chili pepper species (*Capsicum annuum*, *Capsicum baccatum*, *Capsicum chinense*, *Capsicum frutescens*, and *Capsicum pubescens*) across the Neotropics beginning at least 10,000 y ago was an intricate coevolutionary process—with some species undergoing possibly multiple domestication events in the same region (1–7). Genetic studies have 1) contributed greatly to our current understanding of *Capsicum* phylogeny and the identification of the closest wild relative of each domesticate, 2) identified several molecular footprints of artificial selection affecting such traits as seed dormancy, pericarp color, stress and/or defense response, and disease resistance (2, 8–16), and 3) highlighted the blurred boundaries of each domesticated species, an issue that has been noted since the early days of taxonomic research.

The putative ancestral range of the genus *Capsicum*'s most recent common ancestor is proposed to be in the Northern Andes region—encompassing Venezuela, Colombia, Ecuador, and Peru. Dispersion during the mid-Pliocene and Pleistocene, before human arrival, likely brought wild species to the Caribbean, Central America, Mexico, and the United States (17). Notably, the Andean clade, which includes the nonpiquant species *Capsicum lanceolatum* and *Capsicum rhomboideum*, has been largely overlooked in domestication studies despite their presence in Mexico (18, 19). Conversely, the Annuum clade, particularly *C. annuum* and *C. frutescens*, has been the focus of extensive research on domestication. This clade includes a continuum from wild chiles (*C. annuum* var. *glabriusculum*) to semiwild, weedy forms, small landraces, and fully domesticated landrace cultivars (*C. annuum* var. *annuum*), including commercial cultivars (2, 20–24). The wide natural distribution of the wild progenitor *C. annuum* var. *glabriusculum* (preferred taxonomic name following Barboza et al.) extends from the southern United States to northern Bolivia and Brazil (25). Meanwhile, the domestication history of *C. frutescens*, which thrives in natural and anthropogenically influenced environments such as milpas and

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[1]To whom correspondence may be addressed. Email: klchiou@ua.edu or araaguilar@uv.mx.

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orchards, remains largely unexplored despite its similarities to *C. annuum* in distribution and use.

Our research examines the origin and diversification of the domesticated species *C. annuum* var. *annuum* within Mexico (Fig. 1). Currently a dominant force in the global spice trade, this chili pepper species has disseminated across continents, integrating into a multitude of biocultural environments—becoming essential to culinary traditions worldwide (26). Previous research on chili pepper domestication has predominantly relied on modern botanical data encompassing morphological, cytogenetic, genetic, and molecular analyses (7, 11, 16, 20, 21, 27). While these studies provide valuable insights, they frequently result in macrolevel inferences that lack precise contextualization in terms of spatial distribution, temporal frameworks, and inferred past human cultural practices. Traditionally, these investigations have adhered to a model that identifies a "core area" of domestication. This model posits one or more centers where domestication is believed to have initially occurred based on current geographic distributions of extant chili pepper populations and/or the locations of a limited number of early archaeological remains. Even archaeologically driven studies have largely concentrated on unearthing the earliest evidence of chili peppers across the Americas (26, 28–31).

Moreover, even when archaeological data such as chili pepper seeds are incorporated into research, they are often utilized solely for presence/absence data or basic length/width measurements (14, 32). This limited approach has resulted in a fragmented and skewed understanding of the chili pepper's complex history, overemphasizing places where exceptional conditions favor the preservation of botanical remains. As in the case of maize, lowland regions have historically been overlooked in favor of highland areas where plant remains are more archaeologically visible and better preserved. However, as Piperno and Pearsall have pointed out, the closest wild relatives of the domesticated *Capsicum* are predominantly distributed in the lowlands of the American continent (33). This suggests that lowland regions played a critical role in the early domestication process, emphasizing the need to broaden the scope of research to include these ecologically rich, yet historically underexplored areas. Consequently, vast areas with extensive histories of past human habitation and potential interaction with wild chili pepper populations are often neglected. These issues are further compounded by the taxonomic ambiguities within the *Capsicum* genus, particularly *C. annuum* var. *annuum*, and the sampling of gene bank accessions without precise geographic data. These factors hinder our ability to make accurate ancestor–descendant inferences. Therefore, it is crucial for these studies to be thoroughly contextualized to account for the wide distribution and diversity of *C. annuum* cultivars, extending even beyond their regions of origin (11, 16).

Research on the domestication of *C. annuum* var. *annuum* by botanists over the past few decades has predominantly aligned with three major and competing models regarding its domestication in Mexico (Fig. 1). These models reflect diverse scholarly opinions on how and where this domestication process may have unfolded:

(1) Singular Center Model: Advanced by Pickersgill (21), this traditional model argues for a single, distinct origin of domestication. It posits that all domesticated *C. annuum* var. *annuum* can be traced back to one geographical and cultural source. While this model simplifies the narrative, it often overlooks the evidence of widespread chili pepper variation and use across different regions.

(2) Broad Regional Model: Proposed by Loaiza et al. (20), this model suggests that domestication did not occur in a singular

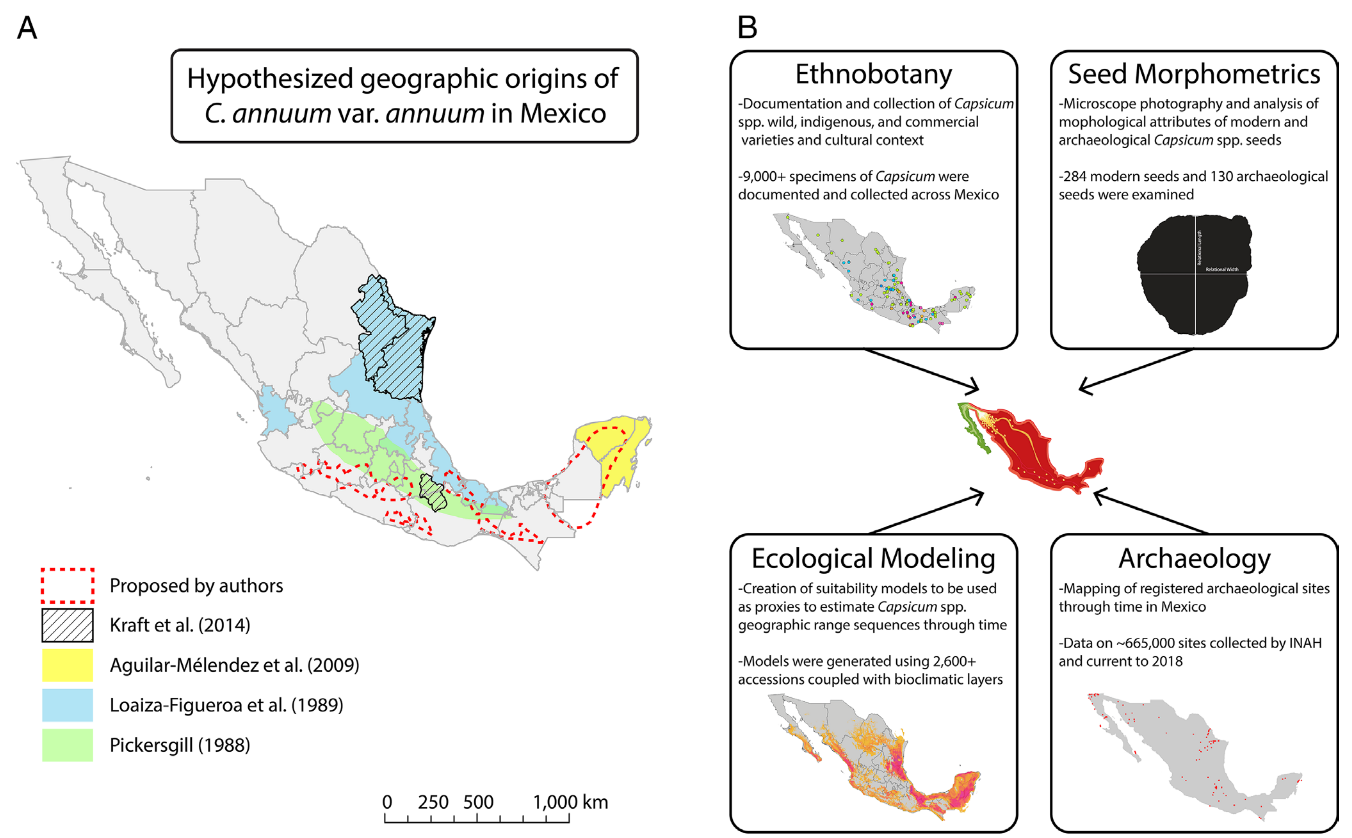

Fig. 1. Overview of *Capsicum* research presented in this paper. A map of Mexico (*A*) features a red dotted line outlining the origins of *C. annuum* var. *annuum* proposed by the authors is based on ecological niche modeling (for *C. annuum* var. *glabriusculum* around 10,000 BP) addressed in Figs. 5 and 6 (50%+ suitability). The multiple lines of evidence used in this study are summarized (*B*).

location. Instead, it identifies a primary center of domestication alongside several secondary loci. This approach acknowledges the complex interactions between human groups and chili peppers across diverse ecological zones, suggesting a more dispersed and interactive model of domestication.

(3) Multiregional Model: Advocated by scholars such as Aguilar-Meléndez et al. (2) and Kraft et al. (32), this model posits that domestication occurred independently in multiple regions. This theory highlights the genetic and cultural diversity *of C. annuum* var. *annuum*, proposing that different human groups may have domesticated local chili pepper varieties in response to distinct regional needs and environmental conditions.

Each of these models is based on the underlying assumption that it is possible to precisely pinpoint the exact times and locations of these domestication events. However, such assumptions may oversimplify the dynamic and complex nature of plant domestication, which is influenced by numerous ecological, cultural, and historical factors. These competing theories not only illustrate the diverse interpretations of archaeological and genetic data but also challenge researchers to consider a broader spectrum of evidence when reconstructing the domestication pathways of this globally significant crop.

Despite the richness of these models, a more holistic and integrated approach to studying the historical and ecological contexts of domestication is necessary. Generally, the reliance on fragmented and regionally biased data has propagated several major misconceptions about the domestication process. For instance, assumptions about the static nature of wild chili pepper populations in their historical ranges ignore the dynamic environmental shifts over millennia that have influenced both plant and human movements. Typically, prior studies on chili pepper domestication have concentrated on identifying traits associated with the domestication syndrome focusing on the extremes of the range, such as increased fruit size and other characteristics that are difficult to trace and define across spatial and temporal boundaries and do not allow for other traits like flavor or flexibility in growing conditions or human preferences to participate in the domestication process (*SI Appendix*, Table S1). Furthermore, the traditional emphasis on male-dominated narratives in agricultural development overlooks the crucial roles women have played in the selection, cultivation, and sharing of chili pepper varieties, particularly in their roles in managing household gardens and local cuisines (34, 35).

This study aims to reframe the narrative of *C. annuum* var. *annuum* domestication and integrate a broader spectrum of archaeological, ethnobotanical, and ecological evidence. By challenging the prevailing hypotheses that focus on specific locales or simplified domestication trajectories, our research offers a more nuanced view of this process. It considers the chili pepper not only as a biological entity but as a key player in the cultural and environmental interactions that have defined human-plant relationships in Mesoamerica. By doing so, we highlight the continuous and interconnected nature of human and chili pepper engagements across time and space. We ask: "**What were the spatial distributions of wild *Capsicum* in the region around modern-day Mexico in the past?**," "**Where were the first encounters of these plants with people?**," and "**When might they have occurred?**" To address these questions, we apply an explanatory framework that integrates multiple lines of evidence that provide the following:

(1) Environmental Context through Ecological Niche Modeling: Ecological niche modeling lends insight into the fluctuating suitability of different regions for various *Capsicum* taxa over time, from the Late Glacial Maximum 20,000 y ago to the present. This modeling was created based on 2,625 records retrieved from herbarium specimens from several sources including data collected by Aguilar-Meléndez.

(2) Cultural Context through Ethnobotany: Ethnobotanical information linked to 284 modern *Capsicum* seed specimens from Mexico, especially landrace cultivars, which are still actively managed by indigenous communities (36) (*SI Appendix*, Fig. S1 and Table S2 and Dataset S1). These modern seeds were analyzed in conjunction with 130 archaeological seeds loaned by various institutions in Mexico and the United States. These archaeological seeds, spanning from the Archaic to the Postcolonial periods (following Mexican independence in 1821), were analyzed using a morphometric approach (*SI Appendix*, Fig. S2 and Table S3).

(3) Multiscalar Spatial Perspectives: At the macroscale, we mapped the ecological niche modeling, all registered archaeological sites across different periods from the Archaic to the present in Mexico, and all geolocations tied to identified *Capsicum* seeds recovered from archaeological sites to pinpoint potential domestication locales (*SI Appendix*, Fig. S3).

Results

Ethnobotanical Data on *Capsicum* in Mexico. Our understanding of *C. annuum* var. *annuum* domestication includes several layers of data and assumptions that need to be critically examined. Before the arrival of humans, the region that is now Mexico featured four taxa (*C. lanceolatum*, *C. rhomboideum*, *C. frutescens*, and *C. annuum* var. *glabriusculum*) (Fig. 2). Although Mesoamerica is traditionally considered the region of origin of major crops such as maize and chili peppers (37), this study extends further north into Mexico to include significant archaeological sites. Of the modern seeds analyzed in this study (*SI Appendix*, Fig. S1 and Table S2), approximately 50% originate from the historical and cultural area of Mesoamerica (38), with more than 80% of this territory situated within Mexico. To ensure a comprehensive and unbiased analysis, a representative sample from across the entire country was included. Most of the seeds measured were from the wild *C. annuum* var. *glabriusculum* and the domesticated *C. annuum* var. *annuum.* We measured 135 seeds from 58 collected fruits of *C. annuum* var. *glabriusculum*, representing 21 states and most of its current geographical distribution. For *C. annuum* var. *annuum*, we analyzed 44 specimens, comprising 67 seed images, including at least 37 landraces and commercial cultivars (Dataset S1).

The research team's primary objective related to modern *Capsicum* material was to obtain seeds that represent the morphological diversity exhibited in Mexico today. Given the dynamic trade and cultivation practices documented among local populations, precise geographic origin was considered less critical for our purposes. Our seed analysis includes samples of both wild and domesticated *C. annuum*—as well as *C. frutescens*—collected from indigenous territories and mestizo areas.

Our study began with an extensive examination of these modern seeds to establish a baseline for comparing them with archaeological samples. This method allows us to integrate cultural dimensions into our scientific inquiry, examining not only the plants in their natural or altered habitats but also the cultural practices surrounding their cultivation and use. Some cultural practices have evolved, yet others, foundational to the genetic alteration of wild chili peppers, continue to persist. This collection, gathered with a focus on ethnobotanical relevance, offers a richer dataset than typical genebank collections. Moreover, our ecological analysis, which includes 2,625 herbarium specimens, enhances the comprehensiveness and relevance of our findings. By combining this detailed ecological data with seed analysis, we create a robust framework for understanding the historical and contemporary contexts of *Capsicum* domestication in Mexico.

***Capsicum* Seed Morphometrics.** Using established methods for *Capsicum* seed identification following Chiou and Hastorf (39), we collected qualitative and quantitative data on 284 modern *Capsicum* seeds from four native species (Dataset S2). Although these seeds were primarily sourced from field collections across Mexico comprising both commercial and landrace cultivars, we also included specimens obtained from herbaria that were originally collected within the country. Additionally, we employed scanning electron microscopy (SEM) to capture detailed images of the seed coats. This analysis revealed a range of surface textures, from the pronounced reticulation found in *C. lanceolatum* and *C. rhomboideum* to the smoother surfaces observed in other taxa (Fig. 2).

Our examination identified 14 morphological attributes exhibiting significant variability, predominantly related to seed size and area (*SI Appendix*, Fig. S4 and Table S4). To further analyze these variations, we conducted a Quadratic Discriminant Analysis (QDA), the results of which are displayed in Fig. 3*A*. The QDA, which included modern specimens represented by colored circles in the figure, successfully predicted the species of 82% of these specimens (*SI Appendix*, Table S5). This high accuracy rate not only reinforces the effectiveness of our morphometric analysis but also supports the distinctiveness of certain species. We see, for example, that *C. rhomboideum* and *C. lanceolatum* can be clearly differentiated from others, aligning with ethnobotanical insights that suggest these species were not historically exploited by humans. Furthermore, the analysis revealed a continuum of characteristics between the fully domesticated *C. annuum* var. *annuum*, its wild progenitor *C. annuum* var. *glabriusculum*, and the semidomesticated *C. frutescens*. This continuum exists irrespective of the specific attributes analyzed, supporting the hypothesis that *C. frutescens*, although managed, is not an entirely independent species but part of a broader domestication spectrum within *C. annuum*. This finding corroborates phylogenetic relationships proposed by previous genetic studies and underscores the nuanced domestication process of these chili peppers, where clear separations exist between commercial and landrace cultivars of *C. annuum*.

Furthermore, we included in our analysis 130 archaeological seeds, denoted by black stars in Fig. 3*A* from pre-Columbian and historic contexts (Dataset S3). These seeds were obtained through the collaboration of various researchers and museums across Mexico and the United States. Most of the seeds were found in association (i.e., relatively dated) with artifacts and/or ecofacts with known dates (*SI Appendix*, Table S3). However, due to the scarcity of chili pepper seeds recovered from archaeological contexts in Mexico and institutional policies, permission to use a destructive absolute dating method was only granted in a few cases. Ultimately, only a few were directly dated using Accelerator Mass Spectrometry radiocarbon dating (*SI Appendix*, Table S6). Despite extensive efforts, we were unable to locate and examine the renowned seed samples from the Tehuacán Valley and Tamaulipas associated with early excavation work led by Richard MacNeish, which are some of the oldest known in the literature (40–42). Our archaeological dataset primarily represents seeds from the Late Archaic to the Preclassic periods. These historical seeds, when plotted alongside modern data, illustrate a morphological trajectory from the wild progenitor *C. annuum* var. *glabriusculum* to the more robust, commercially cultivated varieties of *C. annuum* var. *annuum*, visually depicting the evolutionary progression of these plants (Fig. 3*A*). The identification reveals that *C. frutescens* has been present for at least the past 1000 y, interacting with both wild and domesticated forms of *C. annuum*.

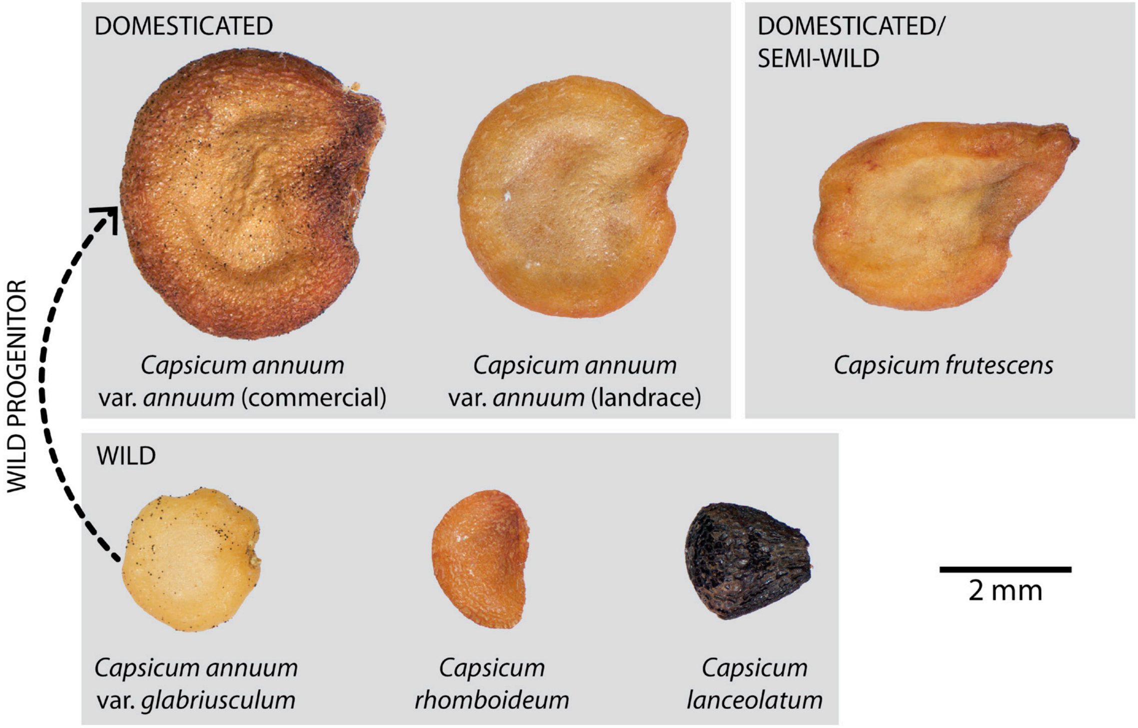

Fig. 2. Domesticated and wild *Capsicum* spp. native to Mexico and their seeds. In the archaeological record, seeds are more frequently recovered than other plant parts (e.g., flowers and fruits) that require extraordinary preservation conditions. To fully leverage these specimens, this project has implemented morphometric approaches for *Capsicum* seed identification. These methods rely on recording seed attributes and measurements; the resulting data assist with interpreting the domestication history of *Capsicum* throughout time.

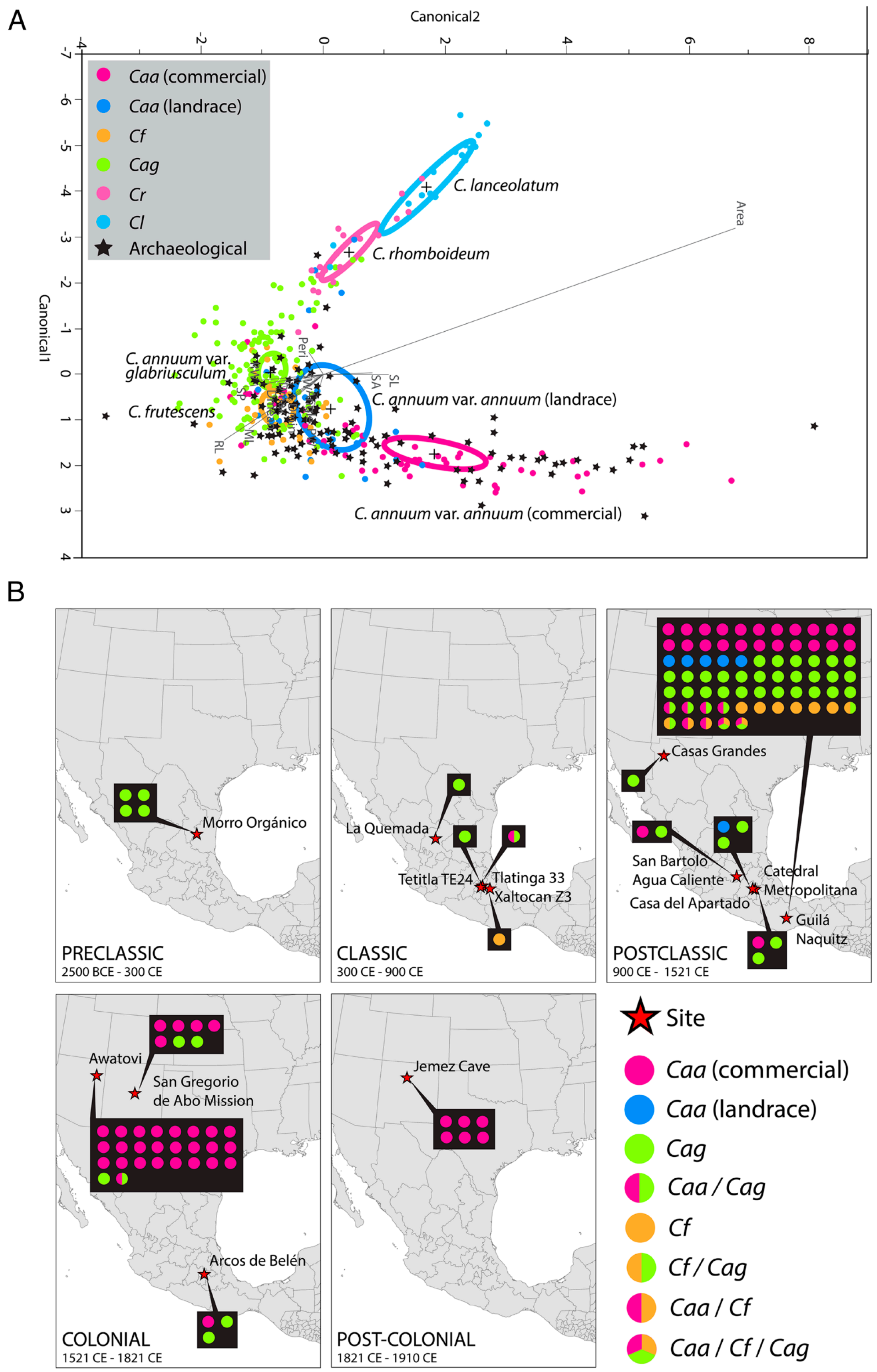

Fig. 3. (*A*) QDA of modern (colored dots) and archaeological (black stars) *Capsicum* seeds. The QDA was used to generate predictive identifications to species-level of (*B*) archaeological seeds sampled for this research.

Changes in *C. annuum* var. *annuum* Morphology over Time. When we input our archaeological seed measurement data into the QDA, the identification predictions included some combinations of two or more taxa (Fig. 3*B*). Organizing the seeds diachronically reveals a clear pattern (Figs. 3*B* and 4). The earliest archaeological samples, dating back to the end of the Late Archaic and the onset of the Preclassic period, predominantly feature seeds identified as the wild progenitor, *C. annuum* var. *glabriusculum*, suggesting widespread use of these chili pepper populations by early peoples. As we progress into the Classic and Postclassic periods, the diversity in seed morphology becomes more pronounced. We observe a variety of seed forms, including those resembling modern commercial cultivars of domesticated *C. annuum* and seeds closely aligned with landrace cultivars. Additionally, many

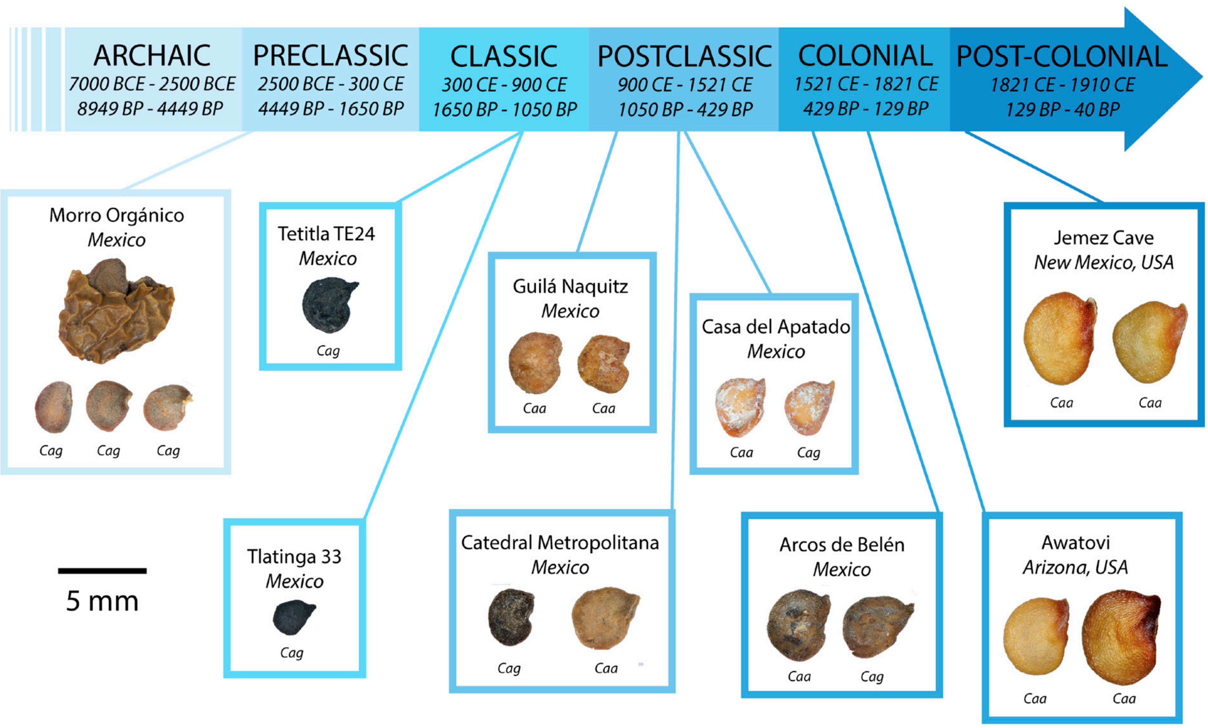

Fig. 4. Temporal sequence of example *C. annuum* var. *glabriusculum* (*Cag*) and *C. annuum* var. *annuum* (*Caa*) archaeological specimens analyzed in this study. While *Caa* seeds in this figure resemble both modern landrace and commercial cultivars, a trend toward larger seed size through time is apparent, a pattern observed archaeologically in other *Capsicum* species such as *C. baccatum* (43). Furthermore, seeds resembling modern *Cag* seeds are present even in Postclassic and Colonial times, suggesting that people continued to use the wild progenitor late in prehistory and into postcontact times.

seeds exhibit characteristics intermediate between the wild progenitor and fully domesticated forms, indicating the presence of hybrid cultivars. This morphological diversity reflects a dynamic and ongoing experimentation and selection by ancient peoples, suggesting a regular understanding and manipulation of *Capsicum* traits. By the time of European contact and thereafter, the seeds predominantly resemble those of modern commercial cultivars, indicating that the traits favored in contemporary agriculture had solidified well before. This later trend toward uniformity in seed morphology implies a shift in selection pressure, possibly influenced by increasing trade and agricultural standardization in Postclassic times.

Changes in *Capsicum* Climatic Suitability over Time. Ecological niche modeling provides crucial insights into the environmental dynamics that have shaped the distribution and domestication of *Capsicum* species. By tracing changes in climatic suitability for three key taxa relevant to humans—*C. annuum* var. *annuum*, *C. annuum* var. *glabriusculum*, and *C. frutescens*—from the Late Glacial Maximum (20,000 y BP) to the present, we have mapped the evolving landscapes that have supported these species through millennia (Fig. 5). The ecological niche models generated for this study illustrate the fluctuating climatic conditions across different regions and how these changes have impacted the suitability for various *Capsicum* taxa. During the Late Glacial Maximum, cooler and drier conditions prevailed, significantly limiting the suitable habitats for these typically warmth-preferring taxa. As the climate warmed and became more humid through the Holocene, we see an expansion in the regions capable of supporting *Capsicum* growth, particularly for *C. annuum* var. *annuum* and *C. frutescens*, which are more adaptable to diverse environmental conditions (44, 45). Even up to the mid-Holocene (6000 BP), however, climactic suitability for all three *Capsicum* species is restricted to the southern half of Mexico.

Placing People and Plants in the Same Place at the Same Time. To find areas where people and chilies intersected at various points in time, we integrated data from all officially registered archaeological sites in Mexico with our ecological niche models. This approach allows us to visualize and analyze the spatial and temporal distribution of human populations in relation to the climatic suitability of *Capsicum* habitats, as depicted in Fig. 6. This map overlays archaeological site distributions with the ecological conditions favorable for *Capsicum*, particularly the wild progenitor, *C. annuum* var. *glabriusculum*. During key periods such as the Late Glacial Maximum, the onset of the Holocene, and the mid-Holocene, we observed a notable proximity between human populations and select regions supportive of wild *Capsicum* growth. Specifically, the Yucatán Peninsula and southern coastal Guerreo emerge as significant areas of interest. Throughout time, these regions maintained climatic suitability for wild *C. annuum*, aligning with the dense concentrations of peoples including the famed ancestral Maya. The consistent suitability of these for *Capsicum* growth, coupled with their archaeological richness, underscores their potential role in the early use and domestication of *Capsicum*. Conversely, Tamaulipas, despite its recognition as a region with high modern diversity of *Capsicum*, shows less promise as an origin point for domestication according to these datasets. The ecological niche models and archaeological evidence suggest that while it may have supported *Capsicum* populations following the mid-Holocene, its role in the earliest phases of domestication may not be as significant as previously thought.

Discussion

A multidisciplinary methodology is essential to address spatial and temporal aspects in order to explore the early stages of chili pepper domestication in Mexico. The impact of preservation and sampling biases on our understanding of *Capsicum* domestication

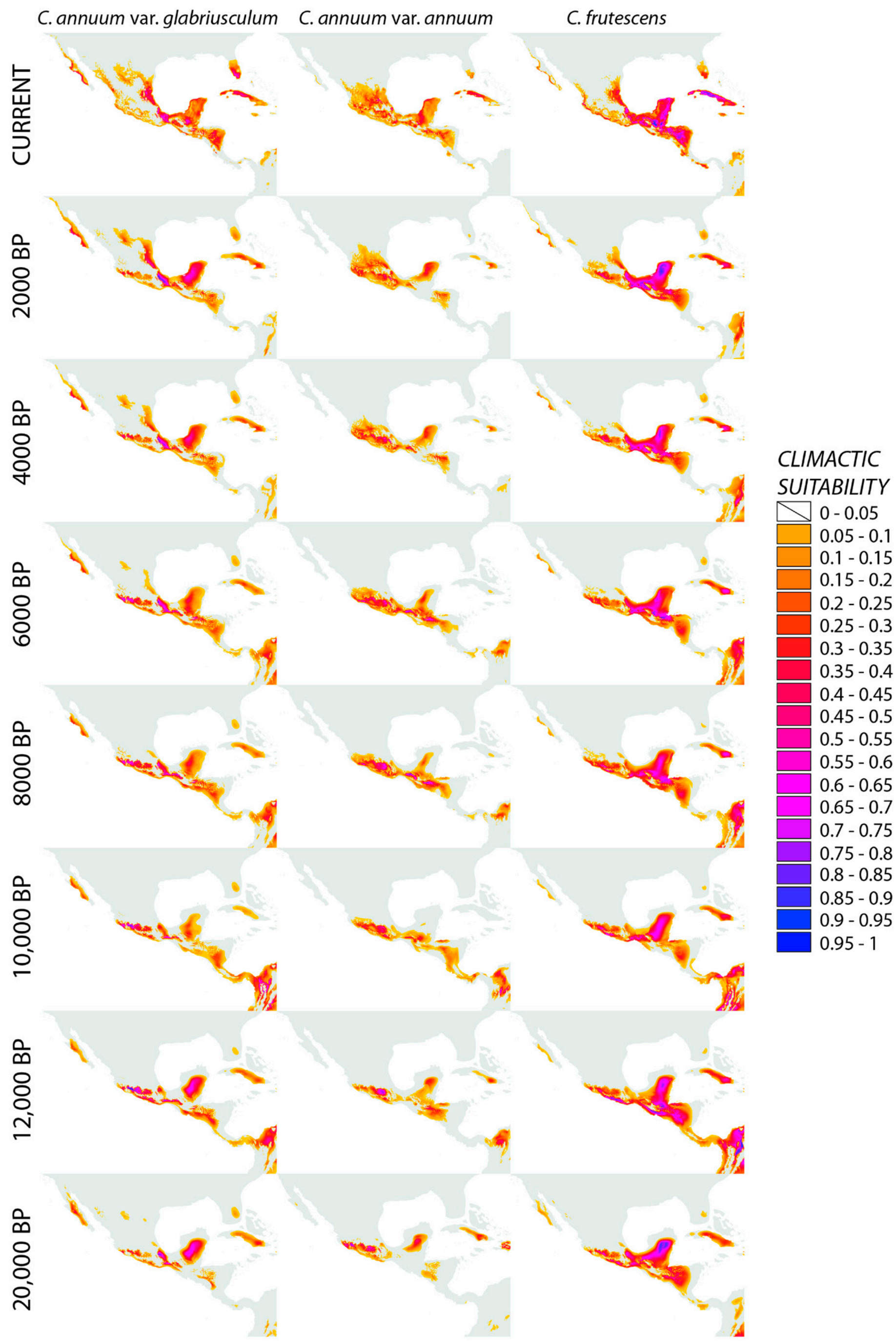

Fig. 5. Changes in climactic suitability for three *Capsicum* taxa (*C. annuum* var. *annuum*, *C. annuum* var. *glabriusculum*, and *C. frutescens*) over time (from 20,000 BP to the present). Suitability values range continuously from 0 (unsuitable, represented by lighter areas on the map) to 1 (highly suitable, represented by darker areas on the map). Climactic suitability was assessed using minimum volume ellipsoid ecological niche models based on 2,625 georeferenced occurrence records and bioclimactic variables derived from transient temperature and precipitation data since the Last Glacial Maximum (CHELSA-TraCE21k v1.0 database). These predictions are based on models selected for their low omission rates, high partial area under the curve (AUC) values, and minimized spatial autocorrelation among occurrence records.

cannot be overstated. These biases affect the visibility of both archaeobotanical materials and archaeological sites, thereby influencing the models based on this evidence. Additionally, contemporary indigenous Mesoamerican peoples, direct descendants of the original domesticators, continue to actively manage and preserve these genetic resources. Their collections, although geographically restricted, have endured throughout history and represent a diversity more closely aligned with real-world conditions than those found in gene banks. Therefore, these collections provide invaluable insights into the complex history of *Capsicum* domestication and are crucial for future studies (13).

Research into the domestication trajectories of plants should not be divorced from conceptualizations of landscape, environment, and cultural/historical contexts (45, 46). Our approach underscores the necessity and promise of a multidisciplinary perspective, incorporating ecology, geography, botany, genetics, archaeology, and anthropology to capture the complex and dynamic processes at play (47). In particular, the application of ecological modeling has provided profound insights into the dynamic interactions between environmental factors and human activities in shaping the domestication of chili peppers. By simulating different climatic and ecological scenarios, we can identify

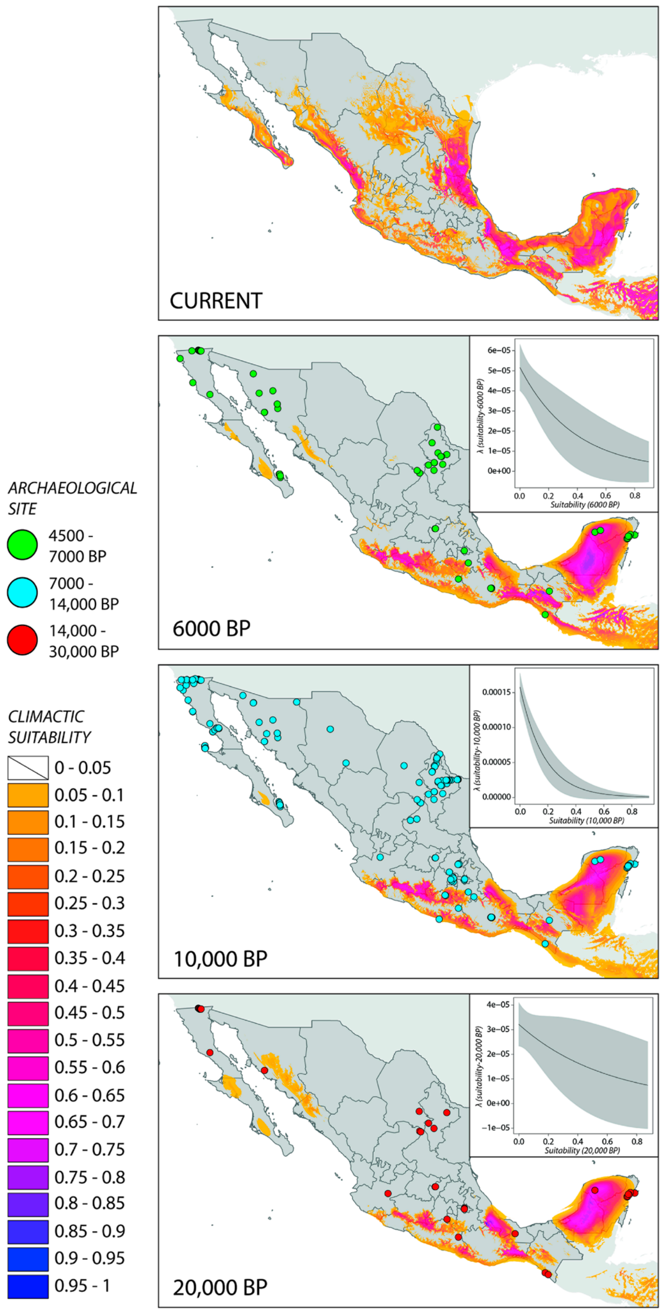

Fig. 6. Registered archaeological sites in Mexico overlaying modern (current), mid-Holocene (6000 BP), early Holocene (10,000 BP), and Last Glacial Maximum (20,000 BP) climatic suitability maps for *C. annuum* var. *glabriusculum*. Insets in the maps for the three oldest climactic suitability predictions display the intensity model of archaeological sites (λ) as a function of the climactic suitability raster for *C. annuum* var. *glabriusculum*, suggesting a nonrandom association between archaeological sites and the climactic suitability for chili peppers. The archaeological sites were grouped by time period using data obtained from Mexico's Instituto Nacional de Antropología e Historia (INAH) site database in 2018.

how changes in habitat suitability have influenced *Capsicum* management and cultivation practices over time. These models help us understand the adaptive responses of *Capsicum* species to environmental pressures and human management, highlighting the importance of ecological factors in guiding the evolution and spread of these plants.

Moreover, this research prompts us to rethink morphological groupings and domestication indicators. Traditionally, studies have dichotomized *Capsicum* morphology into two groups to signify domestication stages: small, upward-facing wild fruits, and larger, hanging domesticated fruits. However, the reality is more nuanced, with a spectrum of forms and flavors ranging from wild to various intermediate stages, such as semiwild and semidomesticated, which have not been adequately considered in past analyses (48). Furthermore, the patterns observed in recent genetic studies are repeated, where *C. frutescens* chili peppers intermingle with wild and domesticates of *C. annuum* (11, 16). Acknowledging this spectrum is crucial for a more accurate representation of *Capsicum* domestication.

Although we know that the species *C. annuum* stands out as the chili pepper being domesticated in Mexico, there is also another native species of domesticated chili pepper that is used in modern Mexico, *C. frutescens* (18, 20). Both are part of the *C. annuum* complex with conflicting phylogenetic relationships, particularly in Mexico (wild and domesticated) *C. annuum* and *C. frutescens* (49, 50): Wild forms "intergrade to such an extent that it is impractical if not impossible to give them distinct taxonomic names." New molecular studies keep recognizing that *C. frutescens* and *C. annuum* are less distinct, possibly reflecting misclassifications or interspecific origins because these two species are cross-fertile (51) or show introgression (52). They are sympatric populations highly appreciated by locals interchangeably in modern times therefore we can assume that chili peppers were utilized in a similar manner in the past (18, 53).

The data also point to significant gene flow among different *Capsicum* species, facilitated by the continual movement and exchange of plant materials among human populations. This gene flow has contributed to the incredible plasticity of the *Capsicum* genus, allowing it to adapt swiftly to diverse environmental and cultural conditions (54, 55). The ability of *Capsicum* species to integrate genetic characteristics from various lineages has undoubtedly been a key factor in their successful domestication and widespread global cultivation. This comprehensive view of *Capsicum* morphology through time not only enhances our understanding of the domestication process beyond its potential locales but also provides insights into the broader evolutionary strategies of plant species under human cultivation.

In summary, our data reveal several areas to be addressed, considered, and be included in future *C. annuum* research:

(1) The geographic distribution of wild chili pepper closest ancestral relatives has often been inaccurately portrayed as static, disregarding environmental changes over time that have altered a region's potential for *Capsicum* first cultivation experiments.
(2) There has been a significant oversight in recognizing the role of cultural practices in domestication processes (e.g., the role of women in the selection and management of wild chili peppers, which has managed and selected the primary gene pool to promote diversity of these plants).
(3) Traditional models have focused primarily on staple crops like maize and beans, leading to a neglect of nonstaple cultigens as well as other regions outside of the conventional agricultural centers of western Mexico and Mesoamerica (1, 2, 16, 32).
(4) Archaeological data have often been limited to early crop findings in a few highland caves, promoting a biased narrative that domestication primarily occurred in these highland locales. This overlooks the extensive human presence across the territory from 35,000 to 10,000 y ago (56–58).
(5) Our multiple lines of evidence suggest that regions like the Yucatán Peninsula, which incidentally are characterized by poor preservation conditions for macrobotanical remains,

should be revisited for early evidence of *Capsicum.* This can be achieved by applying environmental genetics to archaeological site materials.

(6) Additionally, our research indicates that Tamaulipas, a region often cited as a potential domestication origin area, would not have been suitable for *C. annuum* var. *glabriusculum*, making it an unlikely candidate for the beginning of the domestication of this species.

By adopting a multidisciplinary approach to *Capsicum* domestication, this study not only enhances its domestication narrative but also provides a framework for revisiting and refining our understanding of plant-human relationships during the Holocene transition, or possibly earlier on (37). This research advocates for a reevaluation of existing domestication models in the Neotropics and emphasized the importance of including a broader range of direct data and indirect inferences supported by models.

Today, a management gradient is observed from wild to domesticated chili peppers, where there is an overlap of forms and sizes that challenges the idea of a polarized domestication syndrome at two extremes. By recognizing the particularities observed in each seed as the target of both modern and ancestral human selection and considering that these practices likely formed part of the intentionality and knowledge systems of ancestral peoples, it becomes evident that these seeds responded to dynamic and diverse bio/eco/cultural environments (37, 59).

The morphological variations observed suggest that as chili pepper populations arrived in new and diverse ecosystems or landscapes managed by the expanding multiethnic residents, a ruderal pathway was established, setting the stage for the initial domestication of *C. annuum* (45). We concluded that the domestication of *C. annuum* var. *annuum* did not occur within a single defined center. Instead, we propose a protracted and geographically diffuse model of chili pepper domestication (59), involving at least two asynchronous events across Mexico. While it is currently impossible to pinpoint the exact locations or timelines of these events, our findings suggest that the domestication took place in at least two distinct regions. These processes were likely independent but may have occurred concurrently or with some degree of interaction, although the precise timing remains unclear.

Our conclusions are supported by previous work, such as Aguilar-Meléndez (2) and Kraft et al.'s (32) multiregional hypothesis which discusses several locales as potential centers of chili pepper domestication. Additional studies on ancestor–descendant relationships have revealed distinct genetic lineages among domesticated *C. annuum* (2, 8), further supporting the hypothesis of multiple domestication origins. While the evidence points to contemporaneous events in different regions, we cannot definitively confirm this synchrony. What is clear, however, is that the process of *Capsicum* domestication involved multiple independent events across different geographic areas.

Materials and Methods

Morphometric Analysis of Modern Seeds. The research team recorded qualitative and quantitative data on 294 modern *Capsicum* seeds. These seeds were sourced from two distinct locations: directly from the field across Mexico and from specimens with a Mexican provenance available in various herbaria. Following the methodological framework established by Chiou and Hastorf (39), the team employed microscope photography to capture high-resolution images of the seeds. This setup included an Olympus SZ61 stereomicroscope paired with an Olympus DP72 camera. For image processing, photographs were stacked using CombineZP software, which allowed for the integration of multiple focal planes into a single in-focus image. Measurements and calibrations of these images were done using Olympus CellSens software. Additionally, the team employed SEM to capture detailed photographs of the seed coats. Analyses of the collected data identified 14 attributes exhibiting significant variability, primarily related to seed size—including diameter, area, length, width, and perimeter (*SI Appendix*, Table S4).

Morphometric Analysis of Archaeological Seeds. Using the procedure described above, the research team photographed and analyzed 130 archaeological *Capsicum* seeds from 14 sites across Mexico, Arizona, and New Mexico, spanning from the Late Archaic to historic periods. The seeds were accessed from archaeobotanical collections in museums and through collaboration with archaeologists in North America and Mexico. Most seeds were preserved through desiccation, although a few were charred. Prior studies have noted that charring can affect seed size, which is an important consideration for taxa determination and analyzing temporal changes (31). Apart from three specimens from the University of Michigan Museum of Anthropology, all archaeological seeds were dated using relative methods. Permission was granted for destructive absolute dating of the three seeds, although the results, all within the last 1000 y, provided limited insights for this study (*SI Appendix*, Table S6).

Ecological Niche Modeling. The research utilized a three-step ecological modeling process to evaluate the growth environment and historical distribution of modern *Capsicum* taxa across Mexico. This analysis drew on 2,625 records from ethnobotanical fieldwork, Mexican herbaria, Mexico's Sistema Nacional de Recursos Fitogenéticos para la Alimentación y la Agricultura, and Mexico's Sistema Nacional de Información sobre Biodiversidad from the Comisión Nacional para el Conocimiento y Uso de la Bioversidad. For each of the three studied *Capsicum* taxa—*C. frutescens*, *C. annuum* var. *glabriusculum*, and *C. annuum* var. *annuum*—georeferenced occurrences were compiled, with respective totals of 633, 989, and 1,003 unique occurrences. These occurrences were then modeled against bioclimatic variables sourced from the CHELSA-TraCE21k v1.0 database, covering different historical periods and utilizing downscaled transient data for temperature and precipitation since the Last Glacial Maximum. Ecological niche models were constructed using the ntbox R package (*SI Appendix*, Fig. S5) (60), employing minimum volume ellipsoids and a model selection protocol that minimized spatial autocorrelation and overfitting by thinning occurrences within a 20 km radius. The best models, determined by low omission rates and high partial area under the curve values, were used to estimate environmental suitability for the *Capsicum* taxa across the study region. Additionally, point pattern analysis was conducted to assess the relationship between the archaeological site locations and ecological suitability for *C. annuum* var. *glabriusculum* at 6000, 8000, 10000, 12000, and 20000 y ago, using the spatstat package in R (v1.64-1) (61). The analysis compared models assuming the intensity of archaeological site distributions was either dependent on or independent of ecological suitability.

Mapping Archaeological Site Distributions. Permission was granted by Mexico's Instituto Nacional de Antropología e Historia (INAH) to access its comprehensive database of registered archaeological sites up to 2018. Using the geographic coordinates from the database, we generated maps of site locations for the main broad time periods in Mesoamerican chronology using ArcMap 10.8.1. These were overlaid with classified suitability distributions imported as rasters into ArcMap. The exact locations of the sites are not published. While duplications and UTM coordinate errors are present in the database, these issues account for only a minimal percentage of the overall dataset. Given the map scale of the analysis we conducted, such errors do not significantly affect the results.

Data, Materials, and Software Availability. Data associated with this study are available in the supporting information. Partial restrictions to the data and materials apply due to ethical and legal considerations surrounding the sharing of sensitive geographic information. Specifically, the geographic coordinates tied to collection locales for modern specimens and archaeological sites are subject to restrictions. The locations of many archaeological sites included in our study were obtained under specific agreements with Mexico's INAH. These agreements strictly limit the dissemination of geographic coordinates to protect the sites from potential looting and to comply with cultural heritage laws. Furthermore, the collection locales for modern specimens often involve regions inhabited or managed by Indigenous communities, where sharing precise locations could lead to unauthorized access and potential exploitation.

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Author affiliations: [a]Department of Anthropology, The University of Alabama, Tuscaloosa, AL 35487; [b]Red de Estudios Moleculares Avanzados, Instituto de Ecología, A.C., Xalapa, Veracruz 91073, México; [c]Licenciatura de Arqueología, Universidad de Ciencias y Artes de Chiapas, Chiapas 29160, México; [d]Department of Anthropology, University of California, Berkeley, CA 94720; and [e]Centro de Investigaciones Tropicales, Universidad Veracruzana, Xalapa, Veracruz 91050, México

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