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ECOGEOGRAFÍA DE TOMATES SILVESTRES (*Solanum spp.*) EN MÉXICO Y LATINOAMÉRICA

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PRESENTA:

GABRIELA RAMÍREZ OJEDA

BAJO LA SUPERVISIÓN DE:

DR. JUAN ENRIQUE RODRÍGUEZ PÉREZ

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Tesis realizada por la C. **Gabriela Ramírez Ojeda** bajo la supervisión del Comité Asesor indicado, aprobada por el mismo y aceptada como requisito para el obtener el grado de:

DOCTOR EN CIENCIAS EN HORTICULTURA

DIRECTOR:

DR. JUAN ENRIQUE RODRÍGUEZ PÉREZ

ASESOR:

DR. JAIME SAHAGÚN CASTELLANOS

ASESOR:

DR. EDUARDO RODRÍGUEZ GUZMÁN

ASESOR:

DR. JOSÉ LUIS CHÁVEZ SERVIA

LECTOR EXTERNO:

DRA. IRIS E. PERALTA MARTÍNEZ

Chapingo, México, abril, 2022

ECOGEOGRAFÍA DE TOMATES SILVESTRES (*Solanum spp.*) EN MÉXICO Y LATINOAMÉRICA

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DATOS BIOGRÁFICOS

Datos personales

Nombre: Gabriela Ramírez Ojeda.

Fecha de nacimiento: 23 de diciembre de 1988.

Lugar de nacimiento: Guadalajara, Jalisco.

CURP: RAOG881223MJCMJB09.

Profesión: Maestra en Ciencias en Recursos Genéticos y Productividad con especialidad en Fisiología Vegetal. Investigador Titular C en Agrometeorología y Modelaje Ambiental. INIFAP-CIRPAC.

Cédula profesional: 11508330

Desarrollo académico

Licenciatura en Biología (2006-2011). Universidad de Guadalajara.

Maestría en Ciencias en Recursos Genéticos y Productividad – Fisiología Vegetal (2014-2017). Colegio de Postgraduados.

Doctorado en Ciencias en Horticultura (2018-2022). Universidad Autónoma Chapingo.

ECOGEOGRAFÍA DE TOMATES SILVESTRES (*Solanum spp.*) EN MÉXICO Y LATINOAMÉRICA[1]

RESUMEN GENERAL

Los tomates son un grupo de especies Solanaceas de amplia distribución mundial. Este grupo está compuesto por 12 especies silvestres y 4 especies filogenéticamente relacionadas con distribución en Latinoamérica, y la especie *Solanum lycopersicum* L. de alto valor comercial y distribución mundial. La importancia de la especie comercial radica en la derrama económica que genera además de sus amplios beneficios nutraceúticos. Las especies silvestres son reservorios de genes con resistencia y tolerancia a factores bióticos y abióticos. Debido a lo anterior, es importante conocer sus patrones de distribución, características edafoclimáticas y ecológicas. La caracterización ecogeográfica se realizó a partir de las coordenadas geográficas de datos pasaporte de 17 especies y un sistema de información ambiental compuesto por 20 variables climáticas, 1 variable geográfica y 13 variables edáficas con resolución espacial de 1 km^2. A través de Sistemas de Información Geográfica y Análisis Multivariado se determinaron las variables más relevantes para la distribución de este grupo de especies, así como los patrones de agrupamiento entre especies debido a su similitud ambiental. Entre los principales hallazgos se identificó la distribución de *S. lycopersicum* en México, los descriptores ecológicos de las 17 especies y los principales grupos formados de acuerdo a la similitud de colectas en su ambiente de origen. En las colectas de *S. lycopersicum* en México se identificaron 5 grupos climáticamente diferentes y las variables de mayor relevancia fueron las relacionadas con rangos de temperatura y precipitación. En el caso de las especies silvestres y filogenéticamente emparentadas se identificaron 6 grupos climáticamente similares y las variables de mayor contribución fueron las relacionadas con disponibilidad hídrica. Estos resultados constituyen una fuente de información confiable para la identificación de colectas y especies con uso potencial para mejoramiento genético, así como para la generación de estrategias de uso y conservación de estos recursos genéticos.

Palabras clave: *Solanum lycopersicum* L., especies silvestres de tomate, caracterización ecogeográfica, descriptores ecológicos, recursos genéticos.

[1] Tesis de Doctorado en Ciencias en Horticultura, Universidad Autónoma Chapingo
Autor: Gabriela Ramírez Ojeda
Director de tesis: Dr. Juan Enrique Rodríguez Pérez

ECOGEOGRAPHY OF WILD TOMATOES (*Solanum spp*.) IN MEXICO AND LATIN AMERICA[2]

GENERAL ABSTRACT

Tomatoes are a Solanaceae group of species with ample worldwide distribution. This group is composed by 12 wild species and 4 phylogenetically related species with distribution in Latin America, and the specie *Solanum lycopersicum* L. of high commercial value and worldwide distribution. The importance of the commercial species lies in the economic benefits it generates, in addition to its extensive nutraceutical benefits. Wild species are reservoirs of genes with resistance and tolerance to biotic and abiotic factors. Due to the above mentioned, it is important to know their distribution patterns, edaphoclimatic and ecological characteristics. Ecogeographical characterization was performed with the geographic coordinates of 17 species passport data and an environmental information system composed of 20 climatic, 1 geographic and 13 edaphic variables with 1 km^2 spatial resolution. Through Geographical Information Systems and Multivariate Analysis, the most relevant variables for species group distribution were determined, as well as grouping patterns among species due to their environmental similarity. Among the main findings, the distribution of *S. lycopersicum* in Mexico, 17 species ecological descriptors, and main groups formed according to the accessions similarity in their original environment were identified. For *S. lycopersicum* accessions in Mexico, 5 climatically similar groups were identified, and the most relevant variables are those related to temperature and precipitation ranges. In the case of wild and phylogenetically related species, 6 climatically different groups were identified and the variables with the greatest contribution were those related to water availability. These results constitute a reliable source of information for the identification of accessions and species with potential use for genetic improvement, as well as for the generation of strategies for use and conservation of these genetic resources.

Key words: *Solanum lycopersicum* L., wild tomato species, ecogeographic characterization, ecological descriptors, genetic resources.

[2] PhD Thesis of Science in Horticulture, Universidad Autónoma Chapingo
Author: Gabriela Ramírez Ojeda
Advisor: Dr. Juan Enrique Rodríguez Pérez

1. INTRODUCCIÓN GENERAL

Las plantas del género *Solanum* conocidas o comúnmente llamadas tomates comprenden la sección *Lycopersicon* donde se incluye la especie cultivada (*Solanum lycopersicum* L.) y 12 especies silvestres: *Solanum arcanum* Peralta, *Solanum cheesmaniae* (L. Riley) Fosberg, *Solanum chilense* Dunal, *Solanum chmielewskii* (C. M. Rick, Kesicki, Fobes, and M. Holle), D. M. Spooner, G. J. Anderson and R.K. Jansen, *Solanum corneliomulleri* J. F. Macbride, *Solanum galapagense* S.C. Darwin and Peralta, *Solanum habrochaites* S. Knapp and D. M. Spooner, *Solanum huaylasense* Peralta, *Solanum neorickii* D. M. Spooner, G. J. Anderson and R. K. Jansen, *Solanum pennellii* Correll, *Solanum peruvianum* L. and *Solanum pimpinellifolium* L. (Peralta et al., 2008).

Adicionalmente, se reconocen 4 especies como un grupo filogenéticamente emparentado. Dichas especies corresponden a la sección Juglandifolia (*Solanum juglandifolium* Dunal y *Solanum ochranthum* Dunal) y *Lycopersicoides* (*Solanum lycopersicoides* Dunal y *Solanum sitiens* I. M. Johnston (Peralta et al., 2008; Causse et al., 2016; Tropicos.org, 2022).

El tomate (*Solanum lycopersicum* L.) es originario de América y domesticada en México (Rodríguez et al., 2009). Esta especie es una de las hortalizas con mayor difusión en el mundo, después de la papa, y la que genera la mayor derrama económica.

Las especies silvestres de tomate son endémicas del oeste de América del Sur desde Ecuador hasta la región norte de Bolivia y Chile; además de dos especies endémicas de las Islas Galápagos. Sobre las especies filogenéticamente cercanas dos de ellas se distribuyen en Colombia, Ecuador y Perú (*Solanum* sect. *Juglandifolia*) y el resto desde la región sur de Perú hasta el norte de Chile (*Solanum* sect. *Lycopersicoides*) (Peralta et al., 2008).

La amplia distribución de estas especies ha generado gran variabilidad genética debido a las condiciones de clima y suelo donde se desarrolla (Chávez et al., 2011).

En México, el tomate constituye una de las hortalizas más importantes debido a la cantidad de empleos directos e indirectos que genera (Chávez et al., 2011), así como por la captación de divisas (SIAP, 2017).

Durante el proceso de domesticación, el tomate sufrió pérdida considerable en su variabilidad genética (Flores-Hernández et al., 2017a); por lo que se ha recurrido en forma frecuente al uso de germoplasma de poblaciones nativas, silvestres o especies emparentadas para el mejoramiento genético, ya que se asume que poseen genes de interés agronómico como tolerancias a factores bióticos y abióticos adversos (Flores-Hernández et al., 2017b); así como características culinarias y de calidad nutracéutica..

Actualmente se reportan diversos acervos genéticos de tomate conservados *ex situ* e *in situ*; sin embargo, no es precisa la distribución geográfica actual de estos materiales; además, se requiere caracterizar los requerimientos ecológicos y las variables ambientales que determinan su distribución con fines de desarrollar estrategias adecuadas y eficientes para la recolección, estudio, conservación y uso sustentable de estos recursos.

Dichas actividades son apremiantes ante el impacto del cambio climático en el Siglo XXI, ya que modificará los patrones térmicos y pluviales al generar variaciones más extremas, las cuales tendrán severas repercusiones en los sistemas naturales (IPCC, 2007; Ramírez et al., 2014) y en los sistemas de producción de cultivos, posicionando a la agricultura como un sector altamente vulnerable ante los impactos producidos por este fenómeno (FAO, 2007; Ramírez et al., 2014).

Ante este panorama, es indispensable determinar el *status* actual de las áreas de distribución natural de las poblaciones nativas, silvestres y emparentadas de tomate, así como identificar sus patrones de adaptación para incrementar las posibilidades de localizar materiales con tolerancia a factores adversos. Esto promoverá el uso y conservación sustentable de los recursos fitogenéticos de este grupo de especies.

Para lograr este nivel de conocimiento, se requiere contar con información estacional y temporal sobre las condiciones edafoclimáticas de los recursos genéticos del tomate, su historia, la dinámica de su desarrollo y aprovechamiento, así como su disposición y distribución en el espacio (Velázquez et al., 2001; Rosete y Bocco, 2003). Información

que puede ser generada a través de técnicas de observación y análisis en sistemas computarizados, conocidos como Sistemas de Información Geográfica (SIG), los cuales consisten en la captura, ingreso, almacenamiento y análisis de datos; así como la presentación de información resultante, con el propósito de generar información válida para la toma de decisiones en el manejo de recursos fitogenéticos (Rosete y Bocco, 2003; Ruíz et al., 2011).

A través de un análisis ecogeográfico mediante el uso de SIG y técnicas de Análisis Multivariado, es posible conocer el status actual de las áreas de distribución natural, rangos adaptativos y la importancia de los factores y variables ambientales en la distribución de las especies (Elith et al., 2006; Ruíz et al., 2008; Cruz-Cárdenas et al., 2014; Sánchez et al., 2018). Con este enfoque puede estudiarse con mayor certidumbre la interacción entre las condiciones ambientales y los factores bióticos y abióticos prevalecientes en el medio, con los que han evolucionado las especies (Sánchez et al., 2018).

Debido a lo anterior, la presente investigación podrá constituir un modelo de acción que podrá ser aplicado a diferentes especies hortícolas y sus parientes silvestres.

1.1 OBJETIVOS

1. Identificar áreas potenciales de distribución de tomate (*Solanum lycopersicum* L.) en México.
2. Identificar áreas potenciales de colecta de tomates silvestres en México.
3. Identificar los descriptores ecológicos de las 17 especies que conforman el grupo filogenético de tomates.
4. Identificar las variables de mayor importancia en la determinación de la distribución de los tomates en México y de especies silvestres y filogenéticamente relacionadas en Latinoamérica.
5. Identificar colectas de tomates silvestres y filogenéticamente relacionados a *S. lycopersicum* tolerantes a condiciones edafoclimáticas en Latinoamérica.

2. DISTRIBUCIÓN, ADAPTACIÓN Y DIVERSIDAD CLIMÁTICA DE POBLACIONES SILVESTRES Y NATIVAS DE JITOMATE (Solanum lycopersicum L.) EN MÉXICO

DISTRIBUTION, ADAPTATION AND CLIMATIC DIVERSITY OF WILD AND NATIVE TOMATO SPECIES (Solanum lycopersicum L.) IN MEXICO

2.1 RESUMEN

El tomate (*Solanum lycopersicum* L.) es una hortaliza de gran importancia en México y el mundo. El proceso de domesticación de esta especie silvestre a una especie comercial ha contribuido a la pérdida de su acervo genético. Las especies silvestres o emparentadas son reservorios de genes con uso potencial para la generación de variedades tolerantes o resistentes a factores bióticos y abióticos específicos. El objetivo fue determinar la distribución geográfica, descriptores ecológicos y patrones de diversidad y adaptación de 1,296 colectas de tomate nativo de México. Para ello se conformó un sistema de información ambiental compuesto por 20 variables climáticas y 1 variable geográfica con resolución espacial de 1 km^2. Con técnicas multivariadas (Análisis de Componentes Principales (ACP) y Análisis Clúster (AC)) y Sistemas de Información Geográfica (SIG) se identificaron las variables más relevantes para la distribución de las colectas, así como los agrupamientos formados de acuerdo a la similitud ambiental entre estas. El ACP determinó que con los tres primeros CP es posible explicar el 84.1% de la variación total. Las variables de mayor relevancia corresponden a variables estacionales de temperatura y precipitación (B2,B7,B12,B14). El AC reveló la formación de 5 clúster estadísticamente significativos. Los descriptores ecológicos se determinaron clasificando las colectas en Provincias Fisiográficas. Se identificó que los climas de tipo templado (C) son los de mayor frecuencia. Finalmente, la distribución potencial se determinó con el modelo MaxEnt con 10 réplicas por validación cruzada, identificándose zonas con alta probabilidad de presencia de tomate. Estos resultados constituyen una fuente

confiable de información útil para planear sitios de colecta e identificar colectas vulnerables o susceptibles a programas de conservación.

Palabras clave: diversidad climática, tomates silvestres, adaptación climática, *Solanum lycopersicum* L.

2.2. ABSTRACT

Tomato (*Solanum lycopersicum* L.) is a vegetable of great importance in Mexico and the world. The process of domestication of its wild ancestor to a commercial species has contributed to the loss of its gene pool. Wild or related species are reservoirs of genes with potential use for the generation of varieties tolerant or resistant to specific biotic and abiotic factors. The objective was to determine the geographic distribution, ecological descriptors, and patterns of diversity and adaptation of 1,296 collections of native tomato from Mexico. For this, an environmental information system was created, made up of 20 climatic variables and 1 geographic variable with spatial resolution of 1 km^2. Using multivariate techniques (Principal Component Analysis (PCA), Cluster Analysis (CA)) and Geographic Information Systems (GIS), the most relevant variables for distribution of the accessions were identified, as well as the groupings formed according to environmental similarity between these. The PCA determined that with the first three PC it is possible to explain 84.1% of the total variation. The most relevant variables correspond to seasonal variables of temperature and precipitation (B2,B7,B12,B14). CA revealed the formation of 5 statistically significant clusters. The ecological descriptors were determined by classifying the accessions in Physiographic Provinces. It was identified that temperate climates (C) are the most frequent. Finally, the potential distribution was determined with the MaxEnt model with 10 replicates by cross validation, identifying areas with a high probability of tomato presence. These results constitute a reliable source of useful information for planning collection sites and identifying accessions that are vulnerable or susceptible to conservation programs.

Keywords: climatic diversity, wild tomatoes, climatic adaptation, *Solanum lycoperisicum*.

2.3 INTRODUCCIÓN

El tomate (*Solanum lycopersicum* L.), miembro de la familia Solanaceae, es una especie de distribución mundial presente en gran variedad de hábitats (Peralta et al., 2008) asociados a diferentes condiciones de clima y suelo (Chávez et al., 2011). El centro de domesticación de la especie es incierto, debido a la ausencia de evidencias arqueológicas y botánicas, aunque se considera a México, a Perú, o a ambos países como los posibles centros de origen, diversificación y domesticación de esta especie (Rick and Fobes, 1975; Peralta and Spooner, 2007).

El proceso de domesticación del tomate implicó dos transiciones, la primera, ocurrida en Sudamérica, que involucra la derivación de la especie parcialmente domesticada *S. lycopersicum* var. cerasiforme (SLC) a partir de la especie silvestre *Solanum pimpinellifolium*. La segunda transición ocurrió en Mesoamérica a partir de SLC, la cual originó a la especie completamente domesticada *S. lycopersicum* var. *Lycopersicum* generándose especies de frutos más grandes (Blanca et al., 2012; 2015).

Sin embargo, reportes recientes sugieren que el origen de SLC es anterior a su domesticación, ya que muchas características típicas de los tomates cultivados en América del Sur son similares a los de esta especie. Posteriormente, SLC fue disminuyendo su presencia una vez que las formas parcialmente domesticadas se extendieron (Razifard et al., 2020).

Es importante destacar que el origen de la especie es sudamericano, pero la posterior diversificación producto de la domesticación que generó las formas cultivadas ocurrió en Mesoamérica (Bai et al 2007; Mata-Nicolás et al 2020). También es importante destacar que *S. lycopersicum* encontró en México ambientes adecuados para su reproducción y formación de poblaciones estables, que pueden denominarse naturalizadas ya que se comportan como si fueran originarias, y se expandieron en diversos ambientes. Ese germoplasma es de gran interés local y global para el mejoramiento del tomate, y en esta tesis se logra una importante caracterización ecogeográfica, que sirve de base para futuras investigaciones, así como también para

la planificación y gestión de los recursos genéticos relacionados con la seguridad alimentaria.

En México, al ser un centro de diversificación y el más importante en cuanto a la domesticación del jitomate, las poblaciones silvestres son aún muy frecuentes, siendo posible encontrarlas en forma tolerada, fomentada, e incluso cultivada (Rodríguez-Guzmán et al., 2009). Generalmente son anuales; aunque si hay humedad continua y condiciones favorables, pueden manifestarse como perenes. En condiciones ambientales no favorables, raramente persisten por generaciones si no se proporciona manejo agronómico (Peralta et al., 2008; Chávez-Servia et al., 2011).

Como es el caso de los cultivos con éxito comercial a nivel mundial, el jitomate sufrió pérdida considerable en su variabilidad genética durante el proceso de domesticación (Flores-Hernández et al., 2017a; Ladizinsky, 1998). Por ello, se ha recurrido al uso de germoplasma nativo, silvestre y de especies emparentadas para incorporar caracteres de interés agronómico o de calidad de fruto a variedades mejoradas (Flores-Hernández et al., 2017b).

Varias investigaciones han demostrado la presencia de una gran riqueza del germoplasma en el jitomate silvestre de México, tanto a nivel molecular como morfológico (Marín et al., 2021, 2020), en la capacidad antioxidante y metabolismo de isopernoides en fruto (Vela et al. 2019), calidad física y hedónica de fruto (Magallanes et al., 2020).

Existen diversos acervos genéticos silvestres de tomate en México que, al haber estado ante condiciones adversas durante los procesos de adaptación natural, es muy probable que hayan desarrollado mecanismos de resistencia específicos, lo que los hace un recurso muy importante para el desarrollo de nuevas variedades mejoradas, las cuales exigen principalmente características de tolerancia a enfermedades específicas y calidad física y nutraceútica del fruto. A pesar de esta importancia reconocida, es incompleta la información acerca de la distribución geográfica actual del jitomate silvestre en México y de los requerimientos ecológicos que la determinan, información relevante para el diseño de estrategias efectivas de conservación sustentable de los recursos fitogenéticos.

Ante el cambio climático pronosticado para el Siglo XXI, se modificarán significativamente los patrones térmicos y pluviales actuales, lo que generará variaciones más extremas que impactarán severamente en los sistemas naturales (IPCC, 2007; Ramírez-Ojeda et al., 2011), lo que alterará fuertemente la distribución geográfica de las especies, posicionando a los recursos fitogenéticos como un sector altamente vulnerable ante los impactos producidos por este fenómeno (FAO, 2007; Ramírez et al., 2011).

Para lograr el nivel de información requerido con el fin de identificar la distribución potencial actual del jitomate silvestre en México, es necesario el conocimiento espacial y temporal de los recursos a estudiar, su historia, la dinámica de su desarrollo y aprovechamiento, así como su disposición en el espacio (Velázquez et al., 2001; Rosete y Bocco, 2003), con el propósito de mejorar el entendimiento de las interacciones entre las condiciones ambientales y los factores bióticos y abióticos con los que las especies han coevolucionado (Sánchez-González et al., 2018). Para lograr este propósito, se emplean técnicas de observación y análisis en sistemas computarizados, conocidos como sistemas de información geográfica (SIG), los cuales permiten la captura, ingreso, almacenamiento y análisis de datos, así como la presentación de información resultante, con el objetivo de generar información válida para la toma de decisiones (Rosete y Bocco, 2003).

Así, ante la necesidad de conocer el status actual de las áreas de distribución natural de las poblaciones nativas y silvestres de jitomate en México, la presente investigación tuvo como objetivo identificar, a través del estudio de los patrones de adaptación climática, la distribución potencial, los rangos adaptativos y la importancia de los factores climáticos de las especies silvestres y nativas de tomate en México a través de métodos ecogeográficos realizados con herramientas de sistemas de información geográfica.

2.4. MATERIALES Y MÉTODOS

2.4.1 Base de datos

La base de datos con la cual se llevó a cabo la presente investigación se integró con datos pasaporte georreferenciados de *S. lycopersicum* L. Para ello, se recabaron 2,983 coordenadas geográficas contenidas en la Red Nacional de Jitomate, bancos de germoplasma (Centro Nacional de Recursos Genéticos-INIFAP, Banco Nacional de Germoplasma Vegetal-UACH), especímenes de herbarios (Herbario de la Universidad de Guadalajara, Herbario de la Universidad de Ciencia y Artes de Chiapas, Herbario de la Facultad de Biología de la Universidad Michoacana de San Nicolás de Hidalgo, Herbario de la Universidad Autónoma de Querétaro "Jerzy Rzedowski", Herbario Nacional de México (UNAM), Herbario del Colegio de la Frontera Sur, Herbario del Instituto de Historia y Ecología de Chiapas), reportes y artículos científicos (Arellano et al., 2013; Bonilla-Barrientos et al., 2014; Maldonado-Peralta et al., 2016; Velasco-Alvarado et al., 2017; Flores-Hernández et al., 2017) e inventarios de plantas nacionales (Red Mundial de Información sobre Biodiversidad) (REMIB, 2019) e internacionales (Tomato Genetics Resource Center y Global Biodiversity Information Facility) (TGRC, 2013; GBIF, 2019).

Del total de colectas recabadas se descartaron registros con datos atípicos, repetidos, con coordenadas geográficas con poca precisión (menor a 3 decimales) y colectas ubicadas en zona atípicas de la especie, quedando un total de 1,296 registros. La Figura 1 muestra la distribución geográfica de las accesiones empleadas en la presente investigación.

Es necesario mencionar que las colectas fueron identificadas a nivel de variedad taxonómica debido a la poca o nula información de algunos de los registros utilizados.

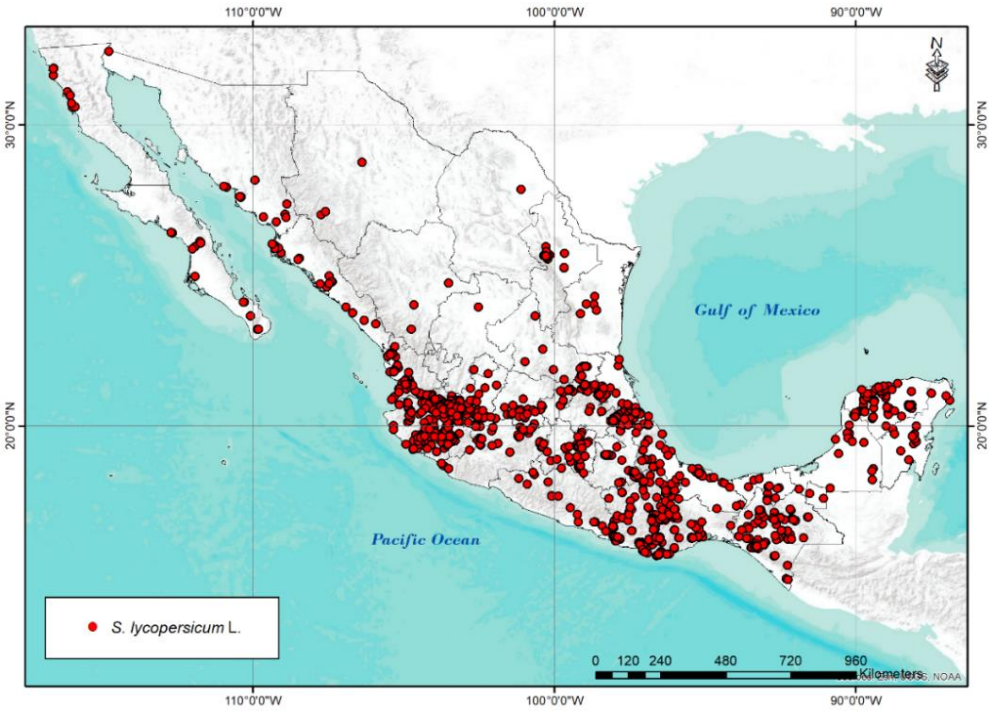

Figura 1. Distribución geográfica de 1,296 colectas de *Solanum lycopersicum* L. en México.

2.4.2 Información climática

Para el presente trabajo se utilizó un sistema de información climática con 20 variables climáticas y 1 variable geográfica, en formato ráster con resolución espacial de 900 m.

Diecinueve variables provienen de las variables bioclimáticas de WorldClim versión 2.1 correspondiente al periodo 1970-2000: B1 (Temperatura media anual, °C), B2 (Rango diurno medio, °C), B3 (Isotermalidad), B4 (Temperatura estacional), B5 (Temperatura máxima del mes más cálido, °C), B6 (Temperatura mínima del mes más frío, °C), B7 (Rango anual de temperatura, °C), B8 (Temperatura media del cuatrimestre más húmedo, °C), B9 (Temperatura media del cuatrimestre más seco, °C), B10 (Temperatura media del cuatrimestre más cálido, °C), B11 (Temperatura media del cuatrimestre más frío, °C), B12 (Precipitación anual, mm), B13 (Precipitación del mes

más húmedo, mm), B14 (Precipitación del mes más seco, mm), B15 (Precipitación estacional), B16 (Precipitación del cuatrimestre más húmedo, mm), B17 (Precipitación del cuatrimestre más seco, mm), B18 (Precipitación del cuatrimestre más cálido, mm) y B19 (Precipitación del cuatrimestre más frío, mm) (Fick and Hijmans, 2017).

Además, se utilizó la evapotranspiración anual (ET, /mm) la cual fue calculada a partir de la suma de los valores mensuales propuestos por Trabucco y Zomer (2019). La altitud del sitio de cada colecta, como variable geográfica, se determinó con un modelo de elevación digital (Fick and Hijmans, 2017).

Las colectas se agruparon de acuerdo a la clasificación de provincias fisiográficas de México (CONABIO, 1997) (Figura 2), con la finalidad de identificar los patrones climáticos de diversidad. Este criterio se empleó para el agrupamiento del AC, descriptores ecológicos y análisis de diversidad climática.

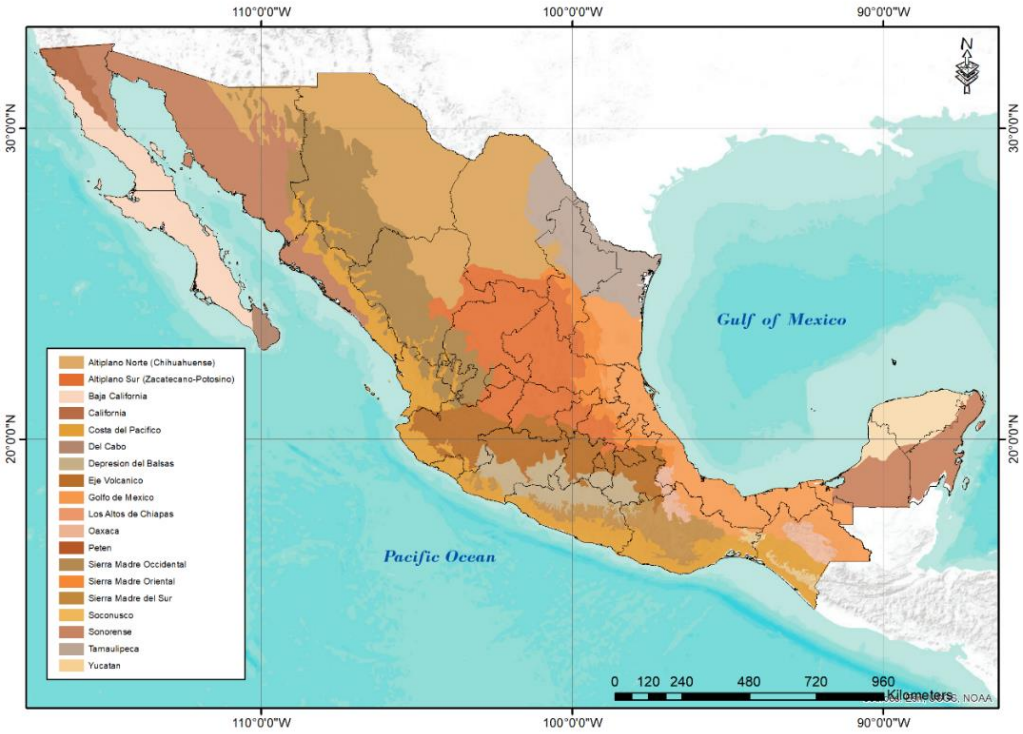

Figura 2. Provincias Fisiográficas de México, CONABIO, 2016.

2.4.3. Análisis estadísticos y descriptores ecológicos

Antes de ejecutar los análisis estadísticos se hizo una selección de variables con el objetivo de identificar alta dependencia lineal (colinealidad) entre más de dos variables. Esta selección de variables se obtuvo a partir de correlaciones de Pearson entre variables, eliminándose aquellas variables con coeficientes absolutos mayores a 0.90.

Con las variables seleccionadas se realizó un Análisis de Componentes Principales (ACP) con una matriz de correlación en RStudio (R Core Team, 2020). El cálculo de eigenvalores, eigenvectores y la contribución de las variables de cada componente principal se obtuvo con los paquetes FactoMineR (Le et al., 2008) y Factoextra (Kassambara, 2017).

Posteriormente se ejecutó un Análisis Clúster (CA) con distancias euclidianas y el método de agrupamiento de Ward de menor varianza para identificar colectas similares. La tendencia de agrupamiento se verificó con la estadística de Hopkins (H) con el paquete clustertend (Yilan and Rutong, 2015), donde valores mayor o igual a 0.5 indican que son muy cercanos y los datos se distribuyen uniformemente, por lo que no tiene sentido el agrupamiento; valores cercanos a 0 son evidencias a favor del agrupamiento de los datos.

La identificación del mejor algoritmo para el agrupamiento se calculó con el paquete clValid (Brock et al., 2008). La selección del número óptimo de clúster se determinó con el paquete NbClust (Charrad et al., 2014). Finalmente se ejecutó un análisis de varianza y prueba de comparación de medias de Tukey entre los grupos identificados en el análisis clúster.

Los descriptores ecológicos se calcularon con la metodología propuesta por Steiner and Greene (1996), y ampliamente utilizada en diferentes especies por Ruiz-Corral et al., 2008; Cerda-Hurtado et al., 2018; Sánchez-González et al., 2018; Ramírez-Ojeda et al., 2021a; 2021b, entre otros.

Para determinar los descriptores ecológicos se utilizó un vector de puntos con las coordenadas geográficas de cada colecta y se determinaron los valores de cada variable. Estos valores se obtuvieron con la herramienta Spatial Analyst Tools de

ArcGis. La información se concentró en una hoja de cálculo donde posteriormente se determinaron los valores extremos (mínimo y máximo), mediana y coeficiente de variación (CV= [Q/Med] *100, where Q= [Q3-Q1]/2 (interquartile range), and Med= median) de cada colecta (Ramírez-Ojeda et al., 2021a). Este proceso se realizó para cada una de las variables seleccionadas.

2.4.4. Diversidad climática y análisis hotspot

Los patrones de diversidad climática se identificaron tomando en cuenta la clasificación de provincias fisiográficas en México.

Para dicho análisis se utilizaron los vectores de coordenadas geográficas de cada colecta y se obtuvo el tipo climático (Tabla 1) de acuerdo a la clasificación climática mundial con el sistema Köppen-Geiger con resolución espacial de ~ 1 km^2 propuesta por Beck et al. en 2018. Con la información obtenida se integró una tabla de frecuencias identificando el número de colectas para cada tipo climático en cada una de las provincias fisiográficas identificadas en las zonas de colecta.

Para el análisis hotspot se identificaron las zonas críticas de abundancia de especies y áreas con alta concentración de diversidad utilizando la herramienta “Spatial Statistics Tools” de ArcGis.

Los mapas de densidad de especies se construyeron al identificar todas aquellas colectas con una distancia entre ellas de 1 km. Esta distancia fue elegida basado en estudios previos de diversidad en especies silvestres de tomate en Sudamérica (Ramírez-Ojeda et al., 2021a) y especies de papa (*Solanum* Sect. *Petota*), grupo hermano de los tomates (Hijmans and Spooner, 2001; Spooner et al., 2010).

El análisis hotspot se ejecutó con la finalidad de determinar el alto (hot) o bajo (cold) agrupamiento espacial de colectas a lo esperado con una distribución aleatoria. El análisis se ejecutó con la estadística Getis-Ord Gi* (Getis and Ord, 1992) para cuantificar las regiones específicas de alto agrupamiento y significancia espacial para la abundancia de colectas y diversidad. La significancia estadística del análisis se calculó usando valores Z.

Tabla 1. Descripción de tipos climáticos con el sistema de clasificación Köppen-Geiger propuesto por Beck et al., 2018.

Tipo climático
Af (tropical y selva), **Am** (tropical y monzón), **Aw** (tropical y sabana), **BWh** (árido, desértico y cálido), **BWk** (árido, desértico y frío), **BSh** (árido, estepa y cálido), **BSk** (árido, estepa y frio), **Csa** (templado, verano seco y cálido), **Csb** (templado, verano seco y cálido), **Csc** (templado, verano frio y seco), **Cwa** (templado, invierno seco, verano cálido), **Cwb** (templado, invierno seco, verano cálido), **Cwc** (templado, invierno seco, verano frío), **Cfa** (templado, sin estación seca, verano cálido), **Cfb** (templado, sin estación seca, verano cálido), **Cfc** (templado, sin estación seca, verano frio), **Dsa** (frío, verano seco y cálido), **Dsb** (frío, verano seco y cálido), **Dsc** (frío, verano seco y frío), **Dsd** (frío, verano seco e invierno muy frío), **Dwa** (seco, invierno seco, verano cálido), **Dwb** (frío, invierno seco, verano cálido), **Dwc** (frío, invierno seco, verano frío), **Dwd** (frío, invierno seco y muy frío), **Dfa** (frío, sin estación seca, verano cálido), **Dfb** (frío, sin estación seca, verano cálido), **Dfc** (frío, sin estación seca, verano frío), **Dfd** (frío, sin estación seca e invierno muy frío), **ET** (polar y tundra), and **EF** (polar y hielo) (Beck et al., 2018)

2.4.5. Distribución potencial

La distribución potencial de tomate en México se determinó con el modelo MaxEnt V. 3.4.4 (Phillips et al., 2022), el cual se basa en el principio de máxima entropía para estimar un conjunto de funciones que relacionan la idoneidad del ambiente con las variables ambientales y determinar la distribución potencial de una especie (Phillips et al., 2006).

Dicho modelo ha sido reconocido por su eficiencia en el manejo de interacciones complejas entre variables predictoras y variables de respuesta (Elith et al., 2011; Fourcade et al., 2014; Sánchez-González et al., 2018).

En cuanto a los parámetros del modelo, se dividieron los datos de ocurrencia aleatoriamente en datos de entrenamiento (50%) y datos de prueba (50%) con la finalidad de probar el ajuste y la significancia estadística del modelo (Ávila et al., 2014). Finalmente, el resultado del modelo se presentó como el modelo ensamble de 10 réplicas por validación cruzada.

El desempeño del modelo se evaluó mediante la estimación del área bajo la curva (AUC), a partir de gráficos de las características operativas del receptor (Hanley and

McNeil, 1982). Dicho estadístico es útil para evaluar la bondad de la selección de las áreas adecuadas contra las áreas no adecuadas para la distribución de tomate, en donde los modelos con AUC mayores a 0.7 son aceptables y con buen rendimiento (Soberón and Peterson, 2011; Sánchez-González et al., 2018).

El modelo ensamble resultante se presentó como un mapa binomial de presencia/ausencia para la distribución de tomates mediante la elección del valor umbral de la aptitud ambiental al seleccionar el valor umbral (Fixed cumulative value 1, Minimum training presence, 10 percentile training presence, máximum training sensitivity plus specificity, etc) que garantice la menor tasa de omisión (áreas conocidas de ocurrencia/ausencia predicha) en un valor logístico máximo (Sánchez-González et al., 2018).

2.5. RESULTADOS Y DISCUSIÓN

2.5.1 Análisis estadísticos y descriptores ecológicos

El análisis de correlación de Pearson determinó que, de las 21 variables empleadas, 10 de ellas no presentaron multicolinealidad, eliminándose el resto de variables para los siguientes análisis estadísticos: B5, B6, B8, B9, B10, B11, B13, B16, B17, B18 y B19.

El ACP determinó que con 3 componentes principales es posible explicar el 84.1% de la variación total entre las colectas. El CP1 (45.6 %) está integrado por B2 (rango diurno medio), B7 (rango anual de temperatura), B12 (precipitación anual), B14 (precipitación del mes más seco) y ET (evapotranspiración anual). Por otra parte, B3 (isotermalidad) y B4 (temperatura estacional) integran el CP2 que corresponde al 22.7 % de la variación total. Finalmente, la altitud (Alt) y temperatura media anual (B1) representan el 15.7% de la variación total entre las colectas.

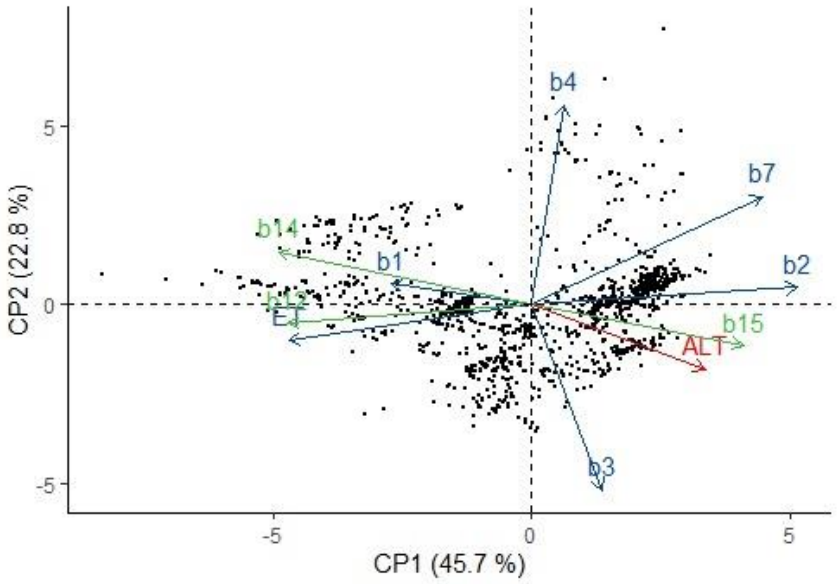

Figura 3. Biplot basado en 10 variables climáticas y 1 variable geográfica en los dos primeros componentes principales (68.5 %). B1 (temperatura media anual), B2 (rango diurno anual), B3 (isotermalidad), B4 (temperatura estacional), B7 (rango anual de temperatura), B12 (precipitación anual), B14 (precipitación del mes más seco), B15 (precipitación estacional), ET (evapotranspiración anual), Alt (altitud). Puntos negros representan las colectas de S. lycopersicum.

Respecto al AC, se utilizó como clase de agrupamiento las provincias fisiográficas previamente mencionadas (Figura 2). Para ello se identificó que 15 de las 19 provincias identificadas en México contienen colectas de S*. lycopersicum*: Altiplano sur (Zacatecano-Potosino), Baja California, Costa del Pacífico, Depresión del Balsas, Eje Volcánico, Golfo de México, Los Altos de Chiapas, Oaxaca, Peten, Sierra Madre del Sur, Sierra Madre Oriental, Soconusco, Sonorense, Yucatán y Tamaulipeca.

El estadístico de Hopkins empleado para evaluar la tendencia al agrupamiento en el conjunto de datos mediante el cálculo de la probabilidad de que los datos correspondan a una distribución normal, mostró evidencias (H= 0.073) de que existen agrupaciones en los datos y que los grupos resultantes serán reales.

El método de agrupamiento elegido de acuerdo al resultado de clvalid fue k-mediodes, con distancias de Gower. Nbclust determinó que el número de grupos óptimos es 5 (Figura 4).

Respecto a los 5 grupos identificados, estos presentan una distribución geográfica bien definida (Figura 4, 5). El grupo 1 se integra por colectas de la zona costera del Pacífico desde el sur de Sonora hasta Chiapas. Este grupo de colectas se distingue por tener mayor distribución a lo largo del país y amplitud en los rangos climáticos y descriptores ecológicos de cada variable (Tabla 2).

El grupo 2 se localizó a lo largo de la zona transvolcánica del país. Estas colectas son las de mayor rango altitudinal y menor temperatura promedio anual. El grupo 3 contiene colectas localizadas en la zona norte del país. Los sitios asociados a estas colectas son las de menor precipitación y evapotranspiración anual.

Las colectas que integran el clúster 4 se localizan a lo largo de toda la costa del Golfo de México, desde Tamaulipas hasta Yucatán. Las zonas donde se localizan estas colectas tienden a tener baja altitud, alta temperatura promedio, precipitación y evapotranspiración anual.

Finalmente, el grupo 5 se localiza en la zona montañosa del este del país, desde el sur de San Luis Potosí hasta Chiapas. Estas colectas se caracterizan por presentarse en sitios con gran altitud, bajas temperaturas promedio y alta disponibilidad hídrica.

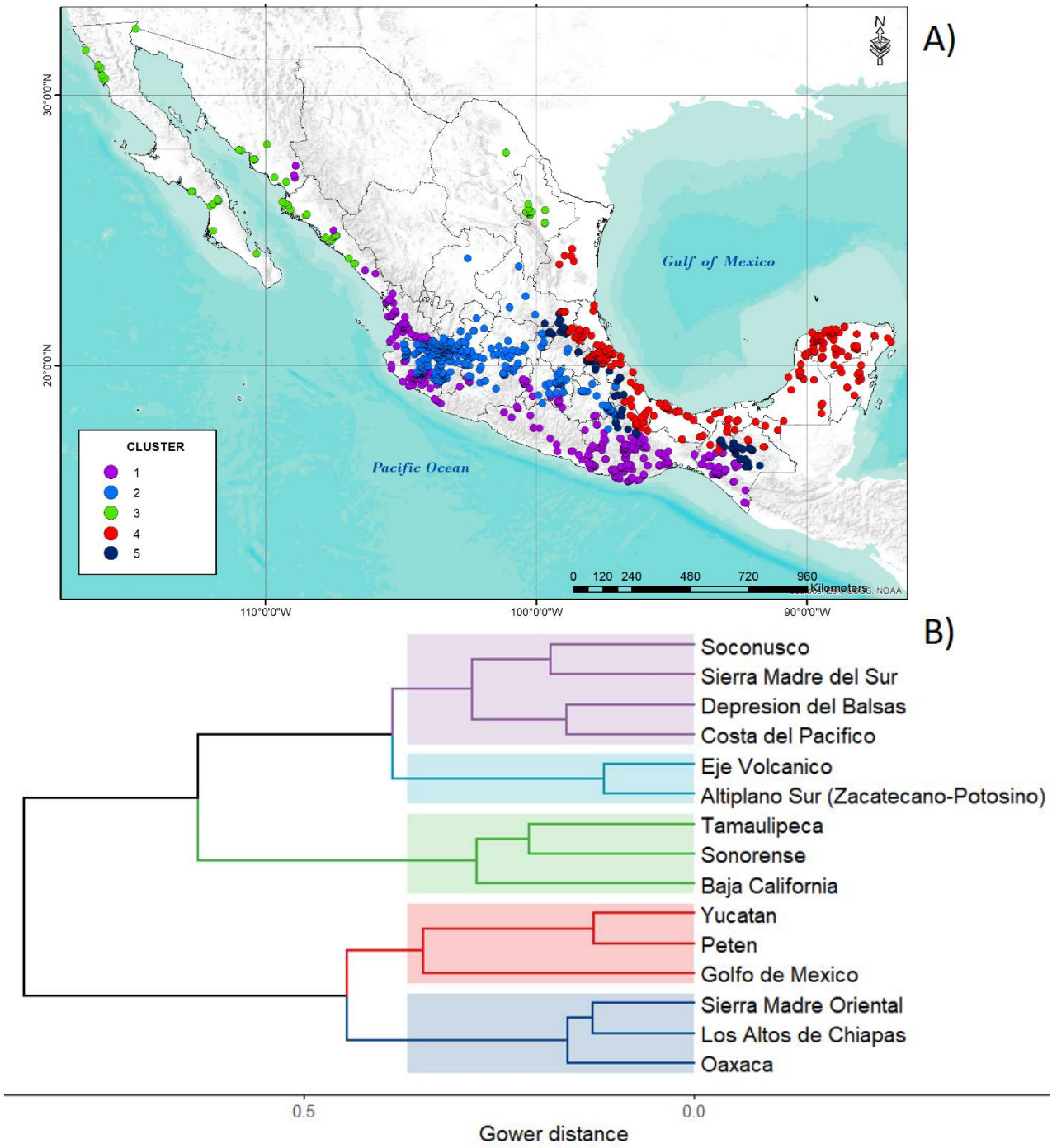

Figura 4. A) Mapa con la distribución geográfica de las colectas de *S. lycopersicum* L. en México de acuerdo a 5 clúster identificados en el AC. **B)** Dendrograma resultados del AC con distancias euclidianas y método de agrupamiento de Ward.

Tabla 2. Descriptores ecológicos de las 10 variables significativas para la distribución de especies de acuerdos a los grupos clúster identificados en el AC. B1 (temperatura media anual), B2 (rango diurno anual), B3 (isotermalidad), B4 (temperatura estacional), B7 (rango anual de temperatura), B12 (precipitación anual), B14 (precipitación del mes más seco), B15 (precipitación estacional), ET (evapotranspiración anual), Alt (altitud). Rango (mínimo-máximo), Med (mediana), CV (coeficiente de variación).

CLUSTER	PROVINCIA FISIOGRÁFICA	PC1														
		B2			B7			B12			B14			B15		
		Rango	Med	CV	Rango	Med	CV	Rango	Med	CV	Rango	Med	CV	Rango	Med	CV
1	Soconusco	11.5-13.3	12.3	3.14	16.0-20.1	17.1	3.22	865-2497	1407	6.04	0-17	2	250	65.5-108.8	105.3	5.2
	Sierra Madre del Sur	9.4-17.8	13.6	14.8	14.4-24.6	19.6	13	414-2938	849	29.93	01-64.0	5	65	76.1-105.3	92.5	2.4
	Depresión del Balsas	13.8-17.3	15.4	4.41	19.8-25.9	23.2	4.71	665-1240	969	3.99	1.0-9.0	3	33.33	93.8-119.5	108.4	1.07
	Costa del Pacífico	9.6-19.1	13.8	10.66	12.8-31.9	20.1	14.17	466-2968	1248	18.96	0-15.0	2	50	82.4-133.9	112.7	5.81
2	Eje Volcánico	11.9-19.5	16.9	5.19	18.6-31.0	26.1	5.94	327-1449	844	8.12	0-36.0	4	37.5	73.6-124.7	110.4	5.87
	Altiplano Sur	13.4-18.7	16.5	6.12	21.2-29.4	25.8	8.43	367-835	592	15.41	2.0-11.0	5	20	67.8-118.3	94.4	15.08
3	Sonorense	12.0-17.9	14.8	4.16	23.7-35.4	25.7	6.6	78-722	402	39.86	0-2.0	1	37.5	49.7-122.4	115.2	4.4
	Tamaulipeca	13.5-15.1	14.3	0.76	27.1-31.8	27.8	2.43	424-815	696	7.51	11.0-21.0	18	5.56	58.6-85.0	80.7	5.47
	Baja California	11.6-18.5	15.9	8.74	19.3-28.6	26.8	9.51	102-294	205	31.52	0-1.0	0	0	70.5-124.8	89.9	7.53
4	Yucatán	10.7-14.9	13.4	4.34	16.1-22.0	19.8	3.47	694-1253	1075	10.57	16.0-39.0	23	8.15	59.1-87.6	67.6	4.78
	Peten	9.7-14.5	12.4	6.49	14.5-20.6	17.5	7.43	1005-1449	1230	6.12	18-43	37	19.57	47.6-84.5	56.1	5.4
	Golfo de México	7.9-14.1	10.5	6.98	15.2-27.7	18.3	5.74	657-3995	1867	15.63	8-141	49.5	26.01	42.4-111.8	66	15.76
5	Sierra Madre Oriental	9.8-14.6	12	3.92	17.3-25.2	20.5	5.37	525-2404	1573	24.95	8.0-56.0	37	25.68	67.4-90.8	78.9	5.59
	Los Altos de Chiapas	10.7-14.1	12.5	6.07	16.8-19.7	18.7	2.81	1045-2376	1390	22.72	3.0-73.0	22	55.68	55.0-93.7	82.4	9.82
	Oaxaca	11.0-16.7	13.1	9.5	17.6-24.8	20.5	7.32	923-3192	1616	36.88	11.0-72.0	34	57.35	70.1-92.4	79.3	9.12

Tabla 2. Continuación.

CLUSTER	PROVINCIA FISIOGRÁFICA	CP1			CP2						CP3					
		ET			B3			B4			B1			ALT		
		Rango	Med	CV	Rango	Med	CV	Rango	Med	CV	Rango	Med	CV	Rango	Med	CV
1	Soconusco	3-121	13	134.6	66.3-75.3	72.1	2.38	93.6-173.8	134	6.63	20.7-23.9	21.9	3.62	839-1396	1141	14.02
	Sierra Madre del Sur	12-310	26	52.4	61.2-79.4	71.5	2.98	83.9-197.8	143	12.6	14.2-22.6	20.3	8.09	1108-2523	1676	10.02
	Depresión del Balsas	18-21	29	12.07	64.4-69.9	67	1.76	135.9-213.8	183	5.01	17.3-28.4	21.9	8.28	243-1940	1320	19.95
	Costa del Pacífico	1-99	37	52.7	55.1-80.0	68.5	3.22	61.4-486.2	175	34.08	19.2-28.4	24.6	5.24	5-1406	550	63.51
2	Eje Volcánico	9-122	34	20.59	59.8-73.0	64.4	2.57	124.3-309.0	240	9.62	13.6-24.5	19.9	6.99	773-2667	1539	14.62
	Altiplano Sur	21-46	27	10.65	59.6-70.1	63.5	1.75	173.6-349.7	272	8.32	15.7-21.9	17.7	3	1002-2344	1939	5.75
3	Sonorense	28-64	52	6.73	46.6-61.9	55.2	6.37	368.6-742.4	487	14.79	22.8-25.5	24.7	1.49	1-139	15	86.67
	Tamaulipeca	43-73	60	4.17	46.3-53.2	50.6	1.44	485.3-644.1	504	3.72	21.1-22.7	22.3	0.76	229-613	504	12.05
	Baja California	32-155	54	63.43	56.8-65.9	60.8	2.72	279.2-499.4	368	13.44	16.0-23.3	21.5	12.17	4-532	86	108.2
4	Yucatán	78-150	100	7.71	63.9-71.5	67.5	1.58	181.8-218.1	196	2.85	25.4-26.6	25.8	0.52	0-124	15	64.6
	Peten	89-203	147	10.63	63.8-74.1	70.3	1.91	154.3-215.4	185	7.01	24.6-26.7	25.9	0.96	6-279	22	243.2
	Golfo de México	31-836	209	23.33	49.5-68.0	56.1	4.47	176.9-509.0	286	16.05	18.2-26.9	24.1	4.34	0-1419	156	79.63
5	Sierra Madre Oriental	34-185	122	24.18	53.2-63.0	59.4	3.21	183.3-368.4	237	20.54	14.5-24.1	19.4	11.09	299-2166	1330	21.71
	Los Altos de Chiapas	20-328	87	67.82	62.5-71.9	67.3	3.84	133.6-203.7	169	7.79	13.4-24.2	19.1	8.83	518-2613	1629	16.04
	Oaxaca	45-290	128	60.16	60.3-68.0	64.8	3.26	191.0-238.9	219	2.82	15.6-24.1	21.1	8.38	549-2078	1275	9.33

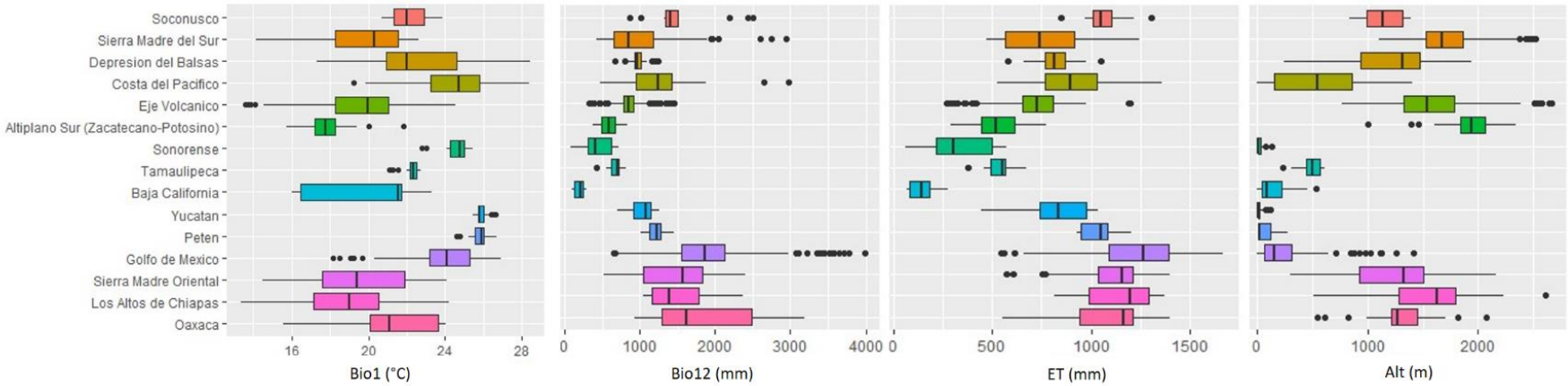

Figura 5. Boxplots de cuatro variables importantes para la distribución de especies silvestres de tomate en México. Bio1 (Temperatura media anual), Bio12 (Precipitación acumulada anual), ET (Evapotranspiración anual), Alt (Altitud).

Respecto a los descriptores ecológicos mostrados en la Tabla 2 y Figura 5, pueden observarse la amplitud climática y correspondencia bien definida de las colectas de tomate distribuidas en cada una de las provincias fisiográficas, y agrupadas de acuerdo a los clústeres identificados en el AC.

Entre los principales hallazgos, destacan las colectas de la zona del Golfo de México presentando mayores valores de precipitación y evapotranspiración anual. El caso contrario (menos disponibilidad hídrica) se presenta en las colectas de la zona de Baja California.

Las colectas de la provincia de Yucatán son las que se presentan en regiones con mayor temperatura media anual y menor altitud y las colectas de la zona del Altiplano Sur (Zacatecano-Potosino) son las de menor temperatura media anual y mayor altitud.

Este tipo de información es de suma importancia ya que ayuda a identificar zonas con la presencia de germoplasma tolerante a ciertas condiciones ambientales, como temperaturas extremas, sequía, exceso de humedad, entre otras.

2.5.2 Diversidad climática y análisis hotspot

De los 30 tipos climáticos reportados por Beck et al. (2018), entre las colectas de tomate en México solo se identificaron 10 de ellos: (Af, Am, Aw, BWh, BSh, BSk, Cwa, Cwb, Cfa y Cfb), predominando los climas de tipo templado (C).

El clima BSh (árido, estepa y cálido) y Aw (tropical, sabana) fueron los que se presentaron en la mayoría de las provincias fisiográficas previamente identificadas. El clima de tipo Af (tropical, selva), fue el de menor abundancia, presentándose solamente en las colectas de la región del Golfo de México y Oaxaca.

En cuanto a la diversidad de climas entre las colectas de cada provincia fisiográfica, las colectas de la región de Peten fueron las que se ubicaron en un solo tipo climático (Aw, tropical, sabana).

Las colectas de la región de Sierra Madre del Sur, Eje Volcánico, Golfo de México, Sierra Madre Oriental y Oaxaca presentan mayor diversidad de climas con 7 tipos.

La Figura 6 muestra la distribución de la diversidad climática para cada provincia de acuerdo a los clústeres previamente identificados en el AC. En este gráfico es posible observar que, dentro de cada grupo, existe bastante similitud climática con diferente proporción entre las provincias fisiográficas que integran cada clúster.

Por otra parte, el análisis hotspot (Figura 7) reveló la presencia de zonas de alta y baja diversidad de manera satisfactoria. Entre las zonas con mayor diversidad o zonas calientes se encuentra prácticamente todas las colectas de Chiapas, la zona límite entre Veracruz con Hidalgo, Querétaro y Puebla, y finalmente una pequeña zona del Estado de México colindante con CDMX y otra pequeña zona del estado de Guerrero. En cuanto a las zonas de importancia debido a la baja diversidad de colectas o coldspot, se localiza la zona norte de Sinaloa, el sur de Veracruz y la zona norte de Jalisco con colindancia a Guanajuato y Michoacán.

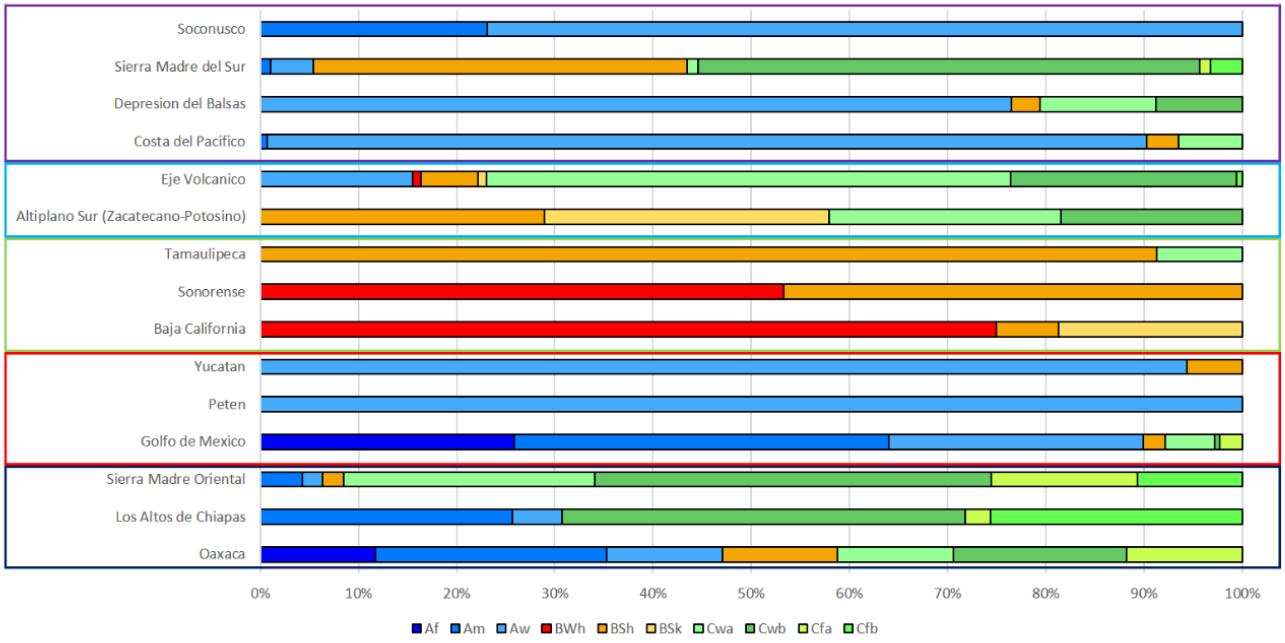

Figura 6. Diversidad climática y porcentaje por tipo climático para las colectas de tomate en México por provincia fisiográfica de acuerdo a los grupos formados por el AC. Tipos climáticos de acuerdo a Beck et al., 2018. Af (Tropical, selva), Am (Tropical, monzón), Aw (Tropical, sabana), BWh (Árido, desértico, cálido), BSh (Árido, estepa, cálido), BSk (Árido, estepa, frío), Cwa (Templado, invierno seco, verano cálido), Cwb (Templado, invierno seco, verano cálido), Cfa (Templado, sin estación seca, verano cálido), Cfb (Templado, sin estación seca, verano cálido). Rectángulo morado= Grupo 1, azul claro= Grupo 2, verde= Grupo 3, rojo= Grupo 4 y azul marino= Grupo 5.

2.5.3 Distribución potencial

La imagen 8 representa la distribución potencial de *S. lycopersicum* en México. El mapa es un modelo ensamble del valor promedio de 10 réplicas por validación cruzada. El valor umbral elegido de acuerdo a la regla de baja tasa de omisión sobre valor logístico máximo en todas las réplicas fue 10 percentile training presence, con un valor promedio de 0.358.

En cuanto al ajuste del modelo, el valor promedio de AUC (área bajo la curva) fue de 0.932, indicando un buen ajuste y desempeño del modelo, al discriminar de manera adecuada las áreas aptas de las no aptas para la distribución de tomate (Phillips et al., 2006).

El modelo de distribución resultante muestra coincidencia en casi todas las regiones donde se ubican colectas, a excepción de la zona norte del país (Baja California, algunas colectas de Chihuahua, Coahuila y Tamaulipas).

En general las zonas de distribución de tomate en México se extienden al norte hasta los 28° por la zona del pacífico y el Golfo de México, cubriendo casi en su totalidad los estados de Sinaloa, Nayarit, Jalisco, Michoacán, Guerrero, Oaxaca, Chiapas, Yucatán, Veracruz y Puebla, quedando sin distribución aparente las zonas más áridas correspondientes a la región del Altiplano y las zonas áridas del norte de la república.

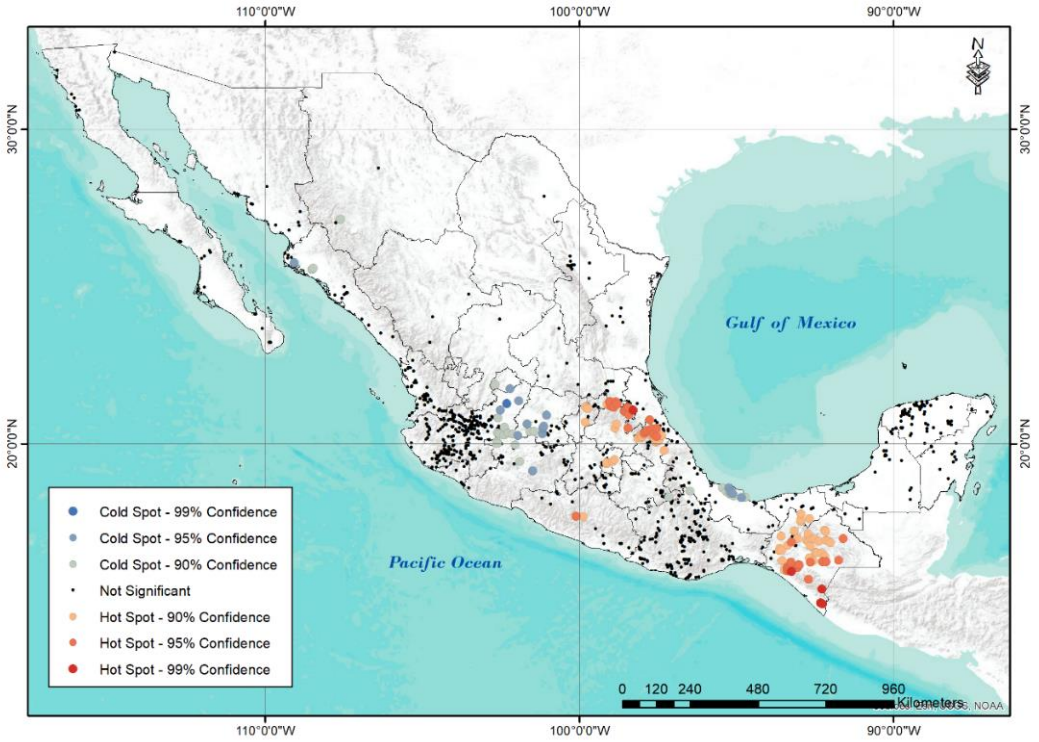

Figura 7. Mapa de distribución potencial de *Solanum lycopersicum* en México

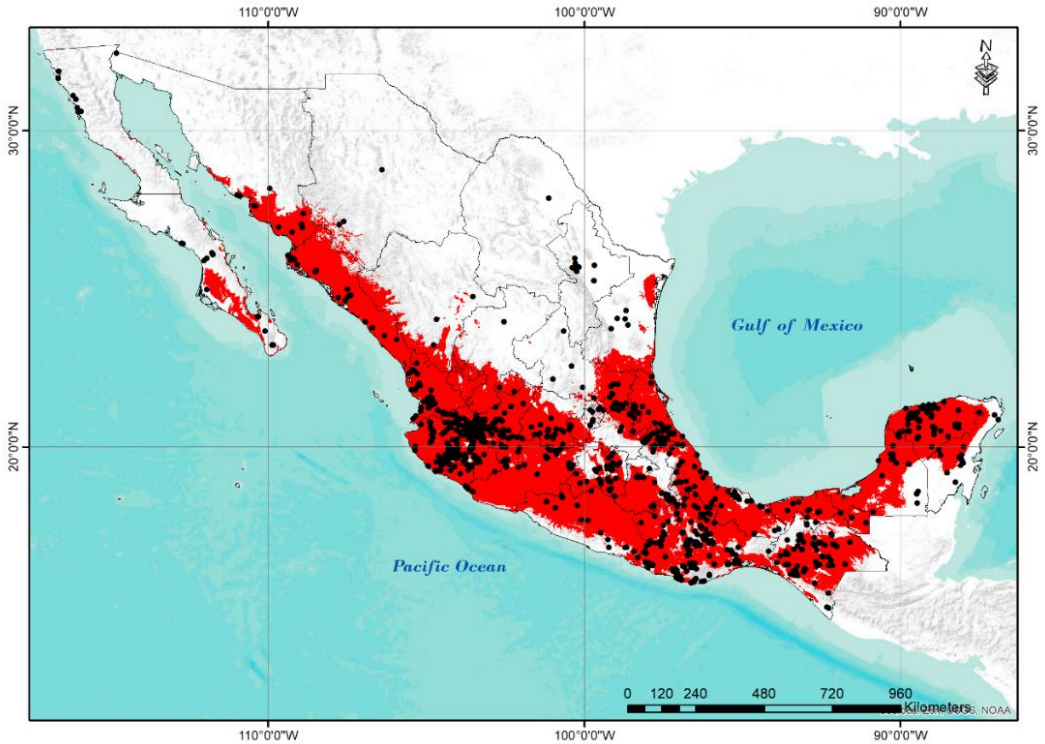

Figura 8. Mapa de abundancia de colectas hotspot (rojo) y coldspot (azul) para 1,296 colectas de *S. lycopersicum* L. en México.

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Article

Climatic Diversity and Ecological Descriptors of Wild Tomato Species (*Solanum* sect. *Lycopersicon*) and Close Related Species (*Solanum* sect. *Juglandifolia* y sect. *Lycopersicoides*) in Latin America

Gabriela Ramírez-Ojeda [1], Iris E. Peralta [2,3], Eduardo Rodríguez-Guzmán [4], José Luis Chávez-Servia [5], Jaime Sahagún-Castellanos [1] and Juan Enrique Rodríguez-Pérez [1,*]

[1] Departamento de Fitotecnia, Universidad Autónoma Chapingo (UACh), Chapingo 56230, Mexico; gabramirezo@gmail.com (G.R.-O.); jsahagunc@yahoo.com.mx (J.S.-C.)
[2] Facultad de Ciencias Agrarias, Universidad Nacional del Cuyo (UNCUYO), Mendoza M5502JMA, Argentina; iperalta@fca.uncu.edu.ar
[3] Centro Científico Tecnológico CONICET, Instituto Argentino de Investigaciones de las Zonas Áridas, Mendoza C1425FQB, Argentina
[4] Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara (UdG), Zapopan 45200, Mexico; edrg@hotmail.com
[5] Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional Unidad Oaxaca, Instituto Politécnico Nacional (IPN) Xoxocotlán, Oaxaca 71230, Mexico; jchavezservia1@yahoo.com
* Correspondence: erodriguezx@gmail.com; Tel.: +52-595-951-7210

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Abstract: Conservation and sustainable use of species diversity require a description of the environment where they develop. The objectives were to determine ecological descriptors and climatic diversity of areas along the distribution range of 12 species of wild tomatoes (*Solanum* sect. *Lycopersicon*) and four wild species of phylogenetically related groups (*Solanum* sect. *Juglandifolia* and sect. *Lycopersicoides*), as well as their ecological similarity in Latin America. With 4228 selected tomato accessions and an environmental information system (EIS) composed of 21 climatic variables, diversity patterns of the distribution areas were identified for each species, as well as ecological descriptors through the use of geographic information systems (GIS). The contribution of climatic variables to the species geographical distribution was identified by principal component analysis (PCA), and similarity in species distribution as a function of the variables identified with cluster analysis (CA). Climatic characteristics and the environmental amplitude of wild tomatoes and related species along their distributional range were satisfactorily determined by ecological descriptors. Eleven climate types were identified, predominantly BSk (arid, steppe, cold), BWh (arid, desert, hot), and Cfb (temperate, no dry season, warm summer). PCA determined 10 most important variables were the most important for the geographical distribution. Six groups of species were identified according to CA and climatic distribution similarity. This approach has shown promissory applications for biodiversity conservation of valuable genetic resources for tomato crop breeding.

Keywords: wild tomato species; ecological descriptors; environmental amplitude; climatic diversity; genetic resources

1. Introduction

Tomato (*Solanum lycopersium* L.), a member of the *Solanaceae* family, is one of the world's leading vegetable crops with worldwide distribution growing in an extensive variety of habitats [1]. Peru has been considered the center of origin, but it is accepted that the tomato diversification process involved two transitions; the first occurred in South America, from the wild species *Solanum pimpinellifolium* L. to a partially domesticated species *Solanum lycopersicum* L. var. *cerasiforme* (SLC); while the second occurred in Mesoamerica from SLC to the completely domesticated species *Solanum lycopersicum* L. var. *lycopersicum*.

However, Razifard et al. [2] recently reported that the origin of SLC may be prior to its domestication since many typical characteristics of tomatoes grown in South America come from this species; later, SLC was lost or diminished once the partially domesticated forms extended toward the north. Further strong artificial selection after the tomato was first introduced to Europe in the XVI century and in modern times greatly reduced the genetic variation of the crop [3]. Wild tomato species related to cultivated tomatoes are valuable resources because they provide genetic diversity due to their ecological adaptation. In addition to the cultivated species, there are 12 species of wild tomatoes (*Solanum* sect. *Lycopersicon* (Mill.) Wettst), and four wild species from two phylogenetically related groups (*Solanum* sect. *Juglandifolia* (Rydb.) A. Child and *Solanum* sect. *Lycopersicoides* (A. Child) Peralta). Wild tomato species of the *Lycopersicon* section are: *Solanum arcanum* Peralta, *Solanum cheesmaniae* (L. Riley) Fosberg, *Solanum chilense* Dunal, *Solanum chmielewskii* (C. M. Rick, Kesicki, Fobes, and M. Holle), D. M. Spooner, G. J. Anderson and R.K. Jansen, *Solanum corneliomulleri* J. F. Macbride, *Solanum galapagense* S.C. Darwin and Peralta, *Solanum habrochaites* S. Knapp and D. M. Spooner, *Solanum huaylasense* Peralta, *Solanum neorickii* D. M. Spooner, G. J. Anderson and R. K. Jansen, *Solanum pennellii* Correll, *Solanum peruvianum* L. and *S. pimpinellifolium* [1], and from the *Junglandifolia* and *Lycopersicoides* sections are *Solanum juglandifolium* Dunal, *Solanum lycopersicoides* Dunal, *Solanum ochranthum* Dunal, and *Solanum sitiens* I. M. Johnston [1,4,5].

A comprehensive treatment of wild tomatoes and close relatives, combining different evidence and their phylogenetic relationships, led to the proposed new classification proposed by Peralta et. al. [1]. The predictability of this classification has been verified in recent studies based on different molecular, genomic, and transcriptomic data of wild tomatoes [3,6,7]. The work of Peralta et. al. [1] has been considered to compare diversity climatic patterns and ecological descriptors. Wild tomatoes, Section Lycopersicon: "Lycopersicon group" (*S. pimpinellifolium*, *S. cheesmaniae* and *S. galapagense*), "Arcanum group" (*S. arcanum*, *S. chmielewskii* and *S. neorickii*), "Eriopersicon group" (*S. habrochaites*, *S. huaylasense*, *S. corneliomulleri*, *S. peruvianum*, and *S. chilense*), "Neolycopersicon group" (*S. pennellii*); outgroup close related species in Section Juglandifolia (*S. juglandifolium* and *S. ochranthum*) and Section Lycopersioides (*S. lycopersicoides* and *S. sitiens*).

Species of *Lycopersicoides* and *Lycopersicon* sections are generally plants that grow in dry habitats along the Pacific coastal range and in inter-Andean valleys, while species of *Junglandifolia* section are distributed in cloudy forests and open areas with high light intensity. Unlike wild species, cultivated tomato is more dependent on humidity and is located in disturbed sites from the tropics, subtropics to temperate zones with defined summers [1].

Wild tomatoes are generally annual; they germinate, grow, reach flowering, fructification, and die in a growing season, but if there is continuous humidity, they manifest as perennials. In other regions, they rarely persist for generations if agronomic management is not provided [1,8].

Breeding programs generally use a limited genetic base, so it is extremely important to explore and know the sources of natural variation [9,10] for identification of genes associated with more rustic characteristics such as resistance to drought [11], extreme temperatures [12], and resistance to pests and diseases [13,14], among others. Likewise, the characteristics of the organoleptic and nutraceutical quality of the fruit have gained importance in the improvement, characteristics that can be found in some wild populations [15,16].

There are various sources of information on the geographical location of tomato species and their gene pools, ex situ and in situ conservation programs, and germplasm banks [17–20]. In addition, some research has been carried out to identify the geographical and ecological patterns of some species [1,21–23]. However, the information on all the wild and related tomato species is scarce since the ecological descriptors and the particular climatic characteristics in which they are distributed are unknown or limited.

Ecogeographic studies of plant genetic resources allow the identification of the adaptive ranges of the species and the most relevant environmental variables that define their distribution [24]. Its main applications are related to the collection, conservation, characterization, documentation, and use of plant genetic resources [7,24–27]. Additionally, it is possible to predict the environmental conditions of the collection sites [11,28,29] from the ecological descriptors derived from the geographical location of germplasm and environmental variables obtained through GIS tools [10,11,28–30].

The central hypothesis of this research postulate that patterns of climatic diversity might coincide with the classification of wild tomatoes reflecting close ancestral relationships.

The objectives were determining the ecological descriptors and the climatic diversity of 16 species (12 species of wild tomatoes (*Solanum* sect. *Lycopersicon*) and four species of phylogenetically related groups (*Solanum* sect. *Juglandifolia* and sect. *Lycopersicoides*)), as well as their ecological similarity in Latin America.

2. Results

2.1. Climatic Diversity

Of the 21 existing climates in Latin America, according to the Köpen-Geiger classification adapted by Beck et al. [31], 12 wild tomatoes and four close related outgroup species were located in 11 of them. Some of the 16 species of the genus *Solanum* showed specific patterns in their distribution within the identified climate types (Figure 1).

The species that presented accessions in the greatest number of climates are *S. habrochaites*, *S. arcanum*, *S. ochranthum*, and *S. juglandifolum*. In contrast, the species with the highest environmental restrictions were *S. sitiens*, *S. lycopersicoides*, *S. corneliomulleri*, and *S. chmielewskii*. Regarding the diversity of climates, those with the greatest predominance among the species are BSk, BWk, and BWh, corresponding to climates of the cold steppe arid type, arid cold desert, and hot arid desert, respectively. Figure 2 shows the distribution and percentage of climates in each species. In this image, the climatic similarity between nearby taxonomic groups derived from phylogenetic data can be observed [1], identifying the same climate types in different proportions for species groups.

2.2. Ecological Descriptors

Ecological zones, as well as the distribution environments and altitudinal ranges reported in the literature for the 16 species of *Solanum* (Sect. Lycopersicon, Juglandifolia, and Lycopersicoides), are shown in Table 1. There were no specific reports of annual mean temperature, annual precipitation, mean diurnal range and annual evapotranspiration, or any other variable in the available literature. In some cases, some climatic parameters associated with the distribution zones are mentioned in general [1,22,23].

The ecological descriptors derived from the geographic location of the accessions and the EIS through the use of GIS tools are shown in Table 2. The variables considered were chosen due to their influence on the establishment of the species: altitude, annual mean temperature, mean diurnal range, annual precipitation, and annual evapotranspiration.

Both the ecological descriptors and the values reported by Peralta et al. [1] and Grandillo et al. [22] show very similar altitudinal ranges. Considering the median altitude values (Table 2) *S. cheesmaniae*, *S. galapagense*, and *S. pimpinelifollium* are the species with the lowest altitudinal range (45–93 m above sea level), and *S. lycopersicoides*, *S. sitiens*, and *S. ochranthum* are the species with the highest altitude range (2740–2928 m above sea level).

The annual mean temperature is a useful variable in the establishment and development of species. It influences, together with other biophysical variables such as relative humidity and precipitation, growth, and productivity of the species.

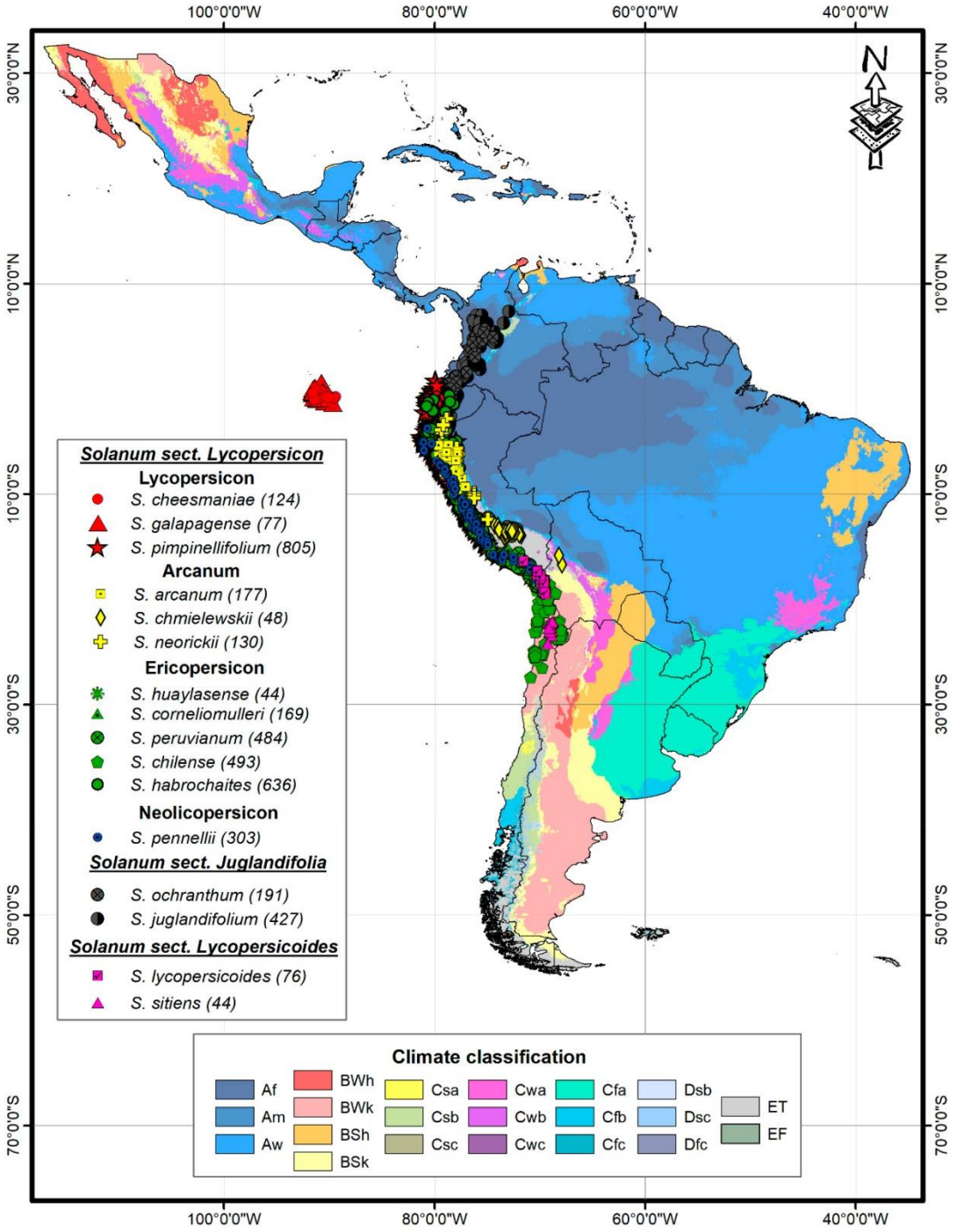

Figure 1. Climate classification according to Beck et al. [31] and geographic distribution of 12 wild tomatoes (Sect. Lycopersicon) and 4 closely related species (Sect. Juglandifolia and Lycopersicoides) Climate classification: Af (tropical, rainforest), Am (tropical, monsoon), Aw (tropical, savannah), BWh (arid, desert, hot), BWk (arid, desert, cold), BSh (arid, steppe, hot), BSk (arid, steppe, cold), Csb (temperate, dry summer, warm summer), Cwb (temperate, dry winter, warm summer), Cfb (temperate, no dry season, warm summer), and ET (polar, frost). In parentheses number of accessions.

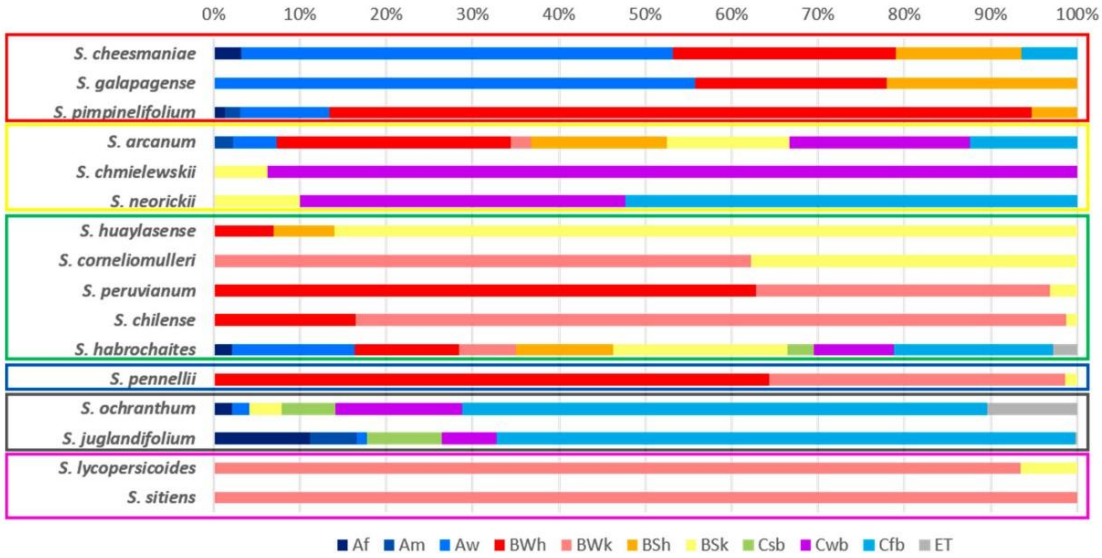

Figure 2. Percentage of climatic type by species according to Beck et al. [31] of 12 wild tomatoes (Sect. Lycopersicon) and 4 closely related species (Sect. Juglandifolia and Sect. Lycopersicoides). Climate classification: Af (tropical, rainforest), Am (tropical, monsoon), Aw (tropical, savannah), BWh (arid, desert, hot), BWk (arid, desert, cold), BSh (arid, steppe, hot), BSk (arid, steppe, cold), Csb (temperate, dry summer, warm summer), Cwb (temperate, dry winter, warm summer), Cfb (temperate, no dry season, warm summer), ET (polar, frost). Within each rectangle, species that belong to the phylogenetic groups proposed by Peralta et al. [1]: Red = Lycopersicon, yellow = Arcanum, green = Ericopersicon, blue = Neoricopersicon, gray = *S.* sect. *Juglandifolia*, pink = *S.* sect. *Lycopersicoides*.

S. cheesmaniae, *S. galapagense*, and *S. pimpinelifollium* are distributed in areas where the median annual mean temperature is above 20 °C, while *S. lycopersicoides* and *S. sitiens* are the species distributed in sites with the lowest annual mean temperature value. The amplitude of the temperature changes, valued by the mean diurnal range, places *S. peruvianum* as the species that are located in places with less thermal oscillation; in contrast, *S. chilense* is located in places with greater thermal oscillation.

S. juglandifolium and *S. ochrantum* require the highest water requirements (annual precipitation and evapotranspiration); in contrast, *S. lycopersicoides* and *S. sitiens* are species characteristics of more arid and drier sites.

2.3. Statistical Analysis

Linear correlation analysis detected multicollinearity between variables BIO6, BIO9-BIO11, BIO16, and BIO17, discarding them (10 variables) from subsequent statistical analyzes. The association patterns between variables were identified using a PCA. Thus, three principal components (PC1, PC2, and PC3) explained 86.2% of the variation, with an individual contribution of 47.8, 27.2, and 11.2%, respectively. Figure 3 shows the biplot of PC1 and PC2 (explaining 75% of the variation), showing the dispersion of the accessions and the contribution of the variables used. PC1 grouped variables related to water and humidity requirements: precipitation of wettest month (BIO13), annual precipitation (BIO12), and annual evapotranspiration (ETPA). PC2 was associated with annual mean temperature (BIO1), mean diurnal range (BIO2), altitude (ALT), mean temperature of the wettest quarter (BIO8), and maximum temperature of the warmest month (BIO5). Finally, PC3 was integrated by the coefficient of variation of seasonal precipitation (BIO15) and isothermality (BIO3).

Table 1. Distribution and altitude (m above sea level) of 16 species of *Solanum* reported in two publications: Peralta et al. [1] and Grandillo et al. [23]. Species described according to taxonomic sections and groups proposed by Peralta et al. [1].

Section/Group	*Solanum* Species	Ecological Distribution	Altitude [1]	Altitude [23]
Section Lycopersicon Lycopersicon	*S. cheesmaniae*	Endemic to the Galapagos Islands. It inhabits dry, open, and rocky slopes, cold places.	0–1300	0–1500
	S. galapagense	Endemic to the Galapagos Islands, on dry, open, and rocky slopes.	0–600 (1500)	0–650
	S. pimpinellifolium	Southern region of Ecuador to the northern region of Chile. Dry slopes, plains, and associated with crop areas.	0–500	0–500
Arcanum	*S. arcanum*	Northern Peru in inter-Andean dry valleys and coastal ecosystems with seasonal fog. Generally dry sites, rocky slopes.	100–2500	500–3000
	S. chmielewskii	Southern zone of Peru and the northern zone of Bolivia. Wet and well-drained rocky slopes.	2300–3000	1600–3100
	S. neorickii	Southern Ecuador to southern Peru, in inter-Andean dry valleys.	1950–3000	1500–2500
Ericopersicon	*S. huaylasense*	Northern and central Peru, on dry, open, and rocky slopes.	1700–000	1000–900
	S. corneliomulleri	Southern Peru in regions with dry and rocky slopes.	1000–3000	1000–3000
	S. peruvianum	Central region of Peru to northern Chile in dry coastal deserts and seasonal mist ecosystems.	0–600	0–2500
	S. chilense	Coastal zone of Chile and northern Peru, on dry rocky slopes, and occasionally saline.	0–3000	50–3500
	S. habrochaites	Andean region of Ecuador and Peru in montane forests and dry slopes, occasionally found in seasonal fog ecosystems.	400–3600	40–3300
Neolicopersicon	*S. pennellii*	North of Peru to the north of Chile, in areas of dry slopes, generally in flat areas.	0–3000	0–1920
Section Juglandifolia	*S. ochranthum*	Andean region of Colombia, Ecuador, and Peru, areas of mountain mesophilic forest.	1900–4100	1200–3200
	S. juglandifollium	Andean region of Colombia, Ecuador, and Peru in areas of mountain mesophilic forest.	1200–3100	1200–3100
Section Lycopersicoides	*S. lycopersicoides*	Southern area of Peru and northern Chile. In ravines and rocky slopes.	1500–3700	1200–3700
	S. sitiens	Hyper-arid areas, northern region of Chile.	2350–3500	2500–3500

Table 2. Ecological descriptors of the wild and related species to *S. lycopersicum*. ALT = altitude, TEMP = annual mean temperature, DRAN = mean diurnal range, RAIN = annual precipitation, EVAPO = annual evapotranspiration. Max = maximum, Min = minimum, Med = median, and CV = coefficient of variation. Species divided according to sections and groups proposed by Peralta et al. [1].

Sections/Group	Species	ALT (m)				TEMP (°C)				DRAN (°C)				RAIN (mm)				EVAPO (mm)			
		Max	Min	Med	CV	Max	Min	Med	CV	Max	Min	Med	CV	Max	Min	Med	CV	Max	Min	Med	CV
Section Lycopersicon	*S. cheesmaniae*	1478	5	87	155.20	25	17.1	23.6	3.27	10.3	7.6	8.5	4.57	562	107	277	21.70	1125	187	454	42.24
	S. galapagense	868	4	45	240.00	25	19.8	23.9	2.87	10.1	7.6	8.7	4.91	546	135	274	16.06	930	262	531	30.60
Lycopersicon	*S. pimpinellifolium*	633	1	93	100.00	26.8	17.9	22.7	8.54	13.3	6.3	9.8	8.37	2989	1	70	157.86	1710	1	45	202.22
Arcanum	*S. arcanum*	3292	132	1681	36.76	24.1	11.4	18.4	9.19	14.4	10.3	12.4	3.42	1193	22	527	43.45	1094	11	395	43.29
	S. chmielewskii	3195	1953	2583	9.52	19.9	13	16.8	9.88	15.6	11.7	14.9	3.21	1318	504	944	18.51	874	429	647	16.74
	S. neorickii	3262	1705	2317	11.57	20.3	11.7	16.9	7.88	15.5	9.9	13.1	2.19	1366	426	816	23.53	1031	326	672	14.29
Eriopersicon	*S. huaylasense*	3124	1141	2291	16.06	20.3	11.2	16.8	8.38	13.9	10.8	13.4	1.27	500	128	346	23.99	416	73	278	30.76
	S. corneliomulleri	3097	1018	2344	18.75	18.3	9.6	14.1	12.95	16.6	9.4	12.3	4.07	434	19	201	60.70	354	12	141	48.58
	S. peruvianum	2617	2	528	124.03	20.9	11.7	18.6	6.98	15.5	4.7	9.4	15.61	434	0	25	92.00	324	0	13	130.77
	S. chilense	3995	0	1904	59.53	20.4	5.4	15.2	19.29	18.6	4.9	12.6	10.82	355	0	28	69.64	275	3	20	72.50
	S. habrochaites	3692	40	2033	33.78	25.8	7	16.6	17.30	14.5	6.5	11.8	5.26	2358	11	622	43.25	1682	8	555	43.69
Neolicopersicon	*S. pennellii*	2921	5	822	53.16	25.1	10.5	18.4	7.38	13.7	6.2	10.2	8.35	404	1	49	95.92	289	0	33	96.97
Section Juglandifolia	*S. juglandifolium*	3353	1005	2195	14.49	22.9	8.9	15.8	10.68	12.5	7.2	9.1	1.94	3214	550	1895	28.79	1648	413	1177	10.24
	S. ochranthum	4008	1195	2750	10.27	21.9	6.7	13.9	11.65	15.6	7.2	11.4	3.42	2358	507	1010	11.44	1474	286	818	13.57
Section Lycopersicoides	*S. lycopersicoides*	3775	1290	2928	13.54	17.3	7.6	11.2	15.28	15.1	10.4	14.1	4.55	215	13	104	53.14	182	9	80	60.94
	S. sitiens	3330	2276	2740	5.90	13.2	8.4	11.4	7.94	17.6	15.6	16.8	1.26	31	8	17	25.00	26	9	21	16.67

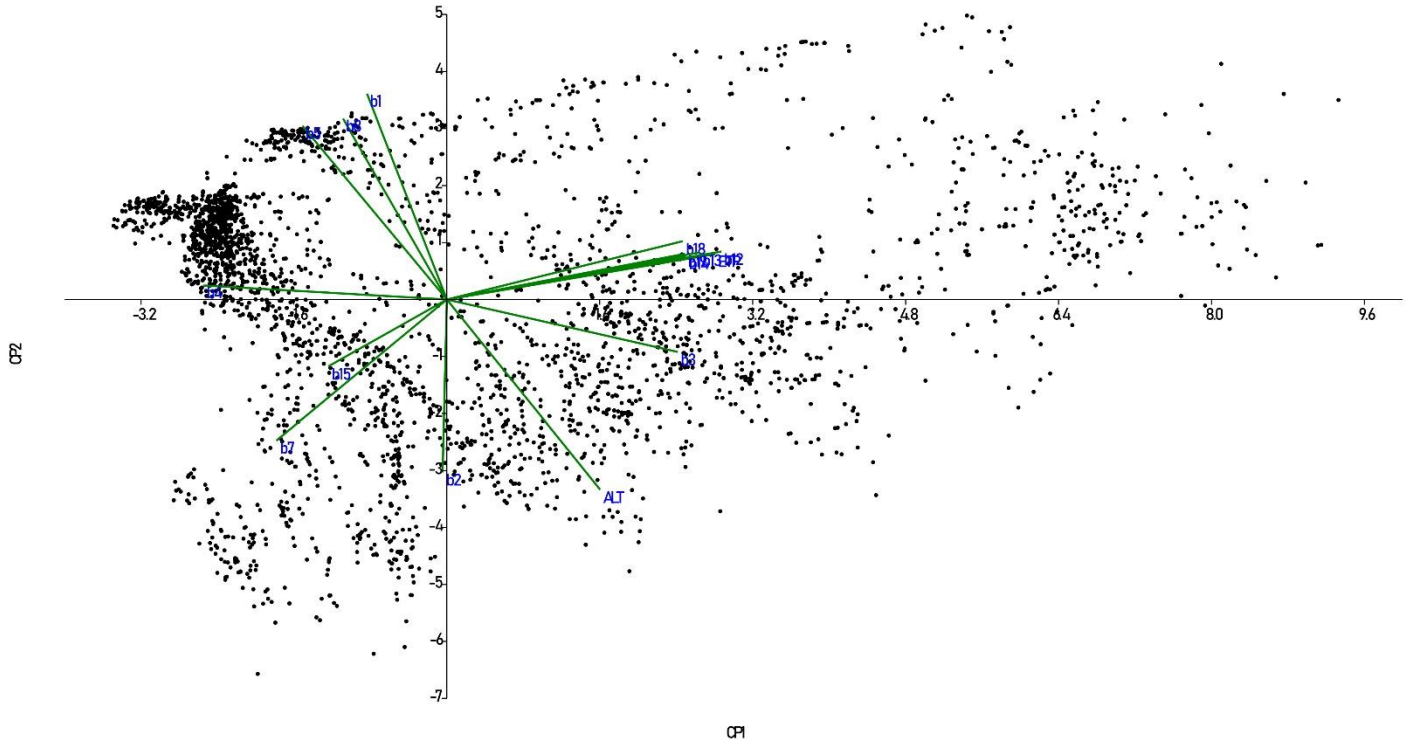

Figure 3. Biplot based on 4228 accessions of wild tomato and related species and 10 climatic variables. BIO13: precipitation of wettest month, BIO12: annual precipitation, ETPA: annual evapotranspiration, BIO1: annual mean temperature, BIO2: mean diurnal range, ALT: altitude, BIO8: mean temperature of wettest quarter, BIO5: maximum temperature of the warmest month, BIO15: coefficient of variation of seasonal precipitation, and BIO3: isothermality. PC1 and PC2 explained 47.8 and 27.2% of the total variation, respectively.

The CA was carried out in order to identify patterns of similarity between accession distribution areas. This analysis included the median values of informative variables previously selected for 67 combinations identified, resulting from the interaction of species by climate type, using the distances of Gower and Ward's grouping method. According to the statistical indicators pseudo-F and pseudo t^2, the number of statistically significant groups was six. In order to corroborate the belonging observations to each identified group, a discriminant analysis was carried out, where the test of restitution of linear discriminant function was applied, which did not indicate changes in the groups generated by the CA, confirming that the classification is reliable. The geographical distribution of the accessions that belong to each group is shown in Figure 4. Table 3 shows the medians and coefficients of variation of each of the groups identified in the CA. The significant variables of the PC were used to describe the groups generated in the CA. From these results, it is possible to identify ecological patterns among the groups formed; for example, the accessions of cluster 1 are those that are found at the highest altitude, and with the lowest annual mean temperature, the species that form cluster 4 and 6 are those with the highest annual precipitation and evapotranspiration, and species of group 1 are located in sites with less availability of humidity. Regarding Kruskal–Wallis non-parametric test of variables for obtained clusters, in all cases, the results were statistically significant ($p \leq 0.001$). Table 4 shows the median values for each cluster, and the corresponding results of rank means comparison of informative variables of 3 PCs.

Table 3. Median (Med) and coefficient of variation (CV) of the ecological descriptors of the combinations of 16 wild and related tomato species by the 11 climatic types identified according to the formation of CA groups. Group = A (Arcanum), E (Ericopersicon), N (Neolicopersicon), Y (Section Lycopersicoides), L (Lycopersicon), and J (Section Juglandifolia). Spe = species, Clim = climate type [31], ALT = altitude, TEMP = annual mean temperature, DRAN = mean diurnal range, RAIN = annual precipitation, EVAPO = annual evapotranspiration. JUG = *S. juglandifolium*, OCH = *S. ochranthum*, CHI = *S. chilense*, COR = *S. corneliomulleri*, HAB = *S. habrochaites*, HUA = *S. huaylasense*, LYC = *S. lycopersicoides*, PEN = *S. pennelli*, ARC = *S. arcanum*, CHM = *S. chmielewskii*, NEO = *S. neorickii*, CHE = *S. cheesmaniae*, GAL = *S. galapagense*, PIM = *S. pimpinelifollium*, PER = *S. peruvianum*, SIT = *S. sitiens*. Climate types: 1 = Af (tropical, rainforest), 2 = Am (tropical, monsoon), 3 = Aw (tropical, savannah), 4 = BWh (arid, desert, hot), 5 = BWk (arid, desert, cold), 6 = BSh (arid, steppe, hot), 7 = BSk (arid, steppe, cold), 9 = Csb (temperate, dry summer, warm summer), 12 = Cwb (temperate, dry winter, warm summer), 15 = Cfb (temperate, no dry season, warm summer), 29 = ET (polar, frost).

Group	CLUTER	Spe-Clim	ALT (msnm)		TEMP (°C)		DRAN (°C)		RAINF (mm)		EVAPO (mm)	
			Med	CV	Med	CV	Med	CV	Med	CV	Med	CV
E	1	CHI-5	2280	44.52	14.1	20.36	13.1	16.98	36	54.17	26	59.62
E	1	CHI-7	3662	12.56	8.1	26.39	14.8	8.26	238	16.81	208	13.73
E	1	COR-5	1989	22.08	15.6	6.65	12	13.81	130	46.15	94	36.9
E	1	COR-7	2637	7.47	11.7	8.4	12.3	2.2	360	9.17	239	15.9
E	1	HAB-29	3558	3.11	9.2	3.38	13.4	4.23	562	1.6	480	18.13
E	1	HAB-5	1805	9.17	15.8	7.66	11.6	2.48	194	16.49	137	28.1
Y	1	LYC-5	2881	13	11.6	13.83	14	4.78	93	59.68	76	61.18
Y	1	LYC-7	3654	0	8.1	0	14.9	0	213	0	182	0.27
N	1	PEN-5	1531	16.98	16.7	4.53	11	6.64	90	56.11	75	46.67
N	1	PEN-7	2526	8.22	12.8	15.18	12.6	1.73	335	11.79	250	14.83
E	1	PER-5	1713	29.19	16	7.72	11.6	12.98	55	104.55	51	77.45
E	1	PER-7	2472	4.69	12.9	3.03	12.3	3.73	339	12.24	213	17.84
Y	1	SIT-5	2740	5.9	11.4	7.94	16.8	0.95	17	25	21	16.67
A	2	ARC-4	679	38.25	20	2.3	11.5	5.29	91	101.1	84	108.33
L	2	CHE-1	620	13.43	21.3	3.6	8.7	8.23	305	7.46	988	6.4
L	2	CHE-15	1013	10.27	19.7	2.61	10	2.72	328	4.81	992	4.39
L	2	CHE-3	144	79.44	23.4	2.12	8.2	4.8	275	16	457	38.29
L	2	CHE-4	47	63.98	24.3	0.69	8.9	1.66	202	22.4	290	7.67
L	2	CHE-6	39	108.97	24.1	1.24	8.4	2.54	359	39.28	504	12.81
E	2	CHI-4	385	90.78	18.7	2.31	9	20.18	7	71.43	7	21.43
L	2	GAL-3	167	81.14	23.4	2.71	8.6	4.7	276	17.93	562	29.36
L	2	GAL-4	20	77.5	24.4	1.27	9.1	4.32	249	18.07	322	39.91
L	2	GAL-6	18	83.33	24.4	0.52	9.3	5.1	275	11.27	531	19.68
E	2	HAB-4	326	110.43	20.6	9.33	11.3	6.28	114	57.46	77	92.86
N	2	PEN-4	622	43.09	19.6	4.5	10	8.15	34	88.24	19	73.68
L	2	PIM-3	27	414.81	25.2	1.42	9.1	5.01	1190	35.88	861	12.31
L	2	PIM-4	95	87.37	22	8.03	10.1	12.63	50	119	25	224
L	2	PIM-6	64	276.38	24.7	2.58	9.8	4.61	602	14.29	485	15.77

Table 3. *Cont.*

Group	CLUTER	Spe-Clim	ALT (msnm)		TEMP (°C)		DRAN (°C)		RAINF (mm)		EVAPO (mm)	
			Med	CV	Med	CV	Med	CV	Med	CV	Med	CV
A	3	ARC-12	2373	9.59	16.3	6.04	13.6	2.39	716	8.1	594	9.6
A	3	ARC-15	2115	13.36	16.8	6.28	12.3	2.43	863	6.55	745	7.99
A	3	ARC-7	2537	17.03	15.1	11.98	13.4	2.46	352	34.23	370	13.24
A	3	CHM-12	2601	9.88	16.7	10.31	15	1.92	948	14.45	663	14.25
A	3	CHM-7	2560	4.02	17.1	4.81	14.3	1.66	534	17.88	449	24.28
E	3	HAB-12	2692	9.68	14.8	9.02	13.7	8.13	761	8.54	645	7.67
E	3	HAB-7	2648	10.84	13.4	12.73	12.9	4.96	393	21.12	296	32.6
E	3	HUA-7	2337	9.99	16.6	5.51	13.6	2.67	354	20.06	282	28.19
A	3	NEO-12	2564	10.26	16.8	9.75	14.6	5.17	999	27.18	626	16.37
A	3	NEO-7	2096	11.09	18.7	8.45	13.8	2.15	541	7.95	419	24.94
J	3	OCH-12	3010	11.05	13.8	10.51	14.4	4.62	967	17.12	664	14.31
J	3	OCH-7	2865	10.12	15	4.04	15.2	10.95	508	25	442	3.73
E	4	HAB-15	2270	8.37	16.1	5.65	11.6	7.69	921	13.74	799	12.52
E	4	HAB-9	2733	12.22	13.9	8.39	11	1.02	595	2.69	582	10.82
J	4	JUG-12	2428	7.91	13.7	4.34	10	6.12	760	18.42	778	8.74
J	4	JUG-29	3144	0	10.9	0	10.7	0	1222	0	1,015	0
A	4	NEO-15	2153	11.18	16.9	6.68	11.8	4.17	817	15.09	719	7.82
J	4	OCH-15	2626	9.12	14	9.08	11.2	8	1041	10.25	825	13.58
J	4	OCH-29	3372	4.09	9.1	6.24	9.9	7.99	1010	6.76	812	11.02
J	4	OCH-9	2725	5.42	13.8	5.12	10.9	6.91	1004	10.48	932	9.87
A	5	ARC-2	1216	0	21.4	0	11.1	0	1193	0	1094	0
A	5	ARC-3	1448	6.01	19.9	2.25	12.2	0.31	694	5.69	537	4.75
A	5	ARC-5	1828	6.44	17.3	2.77	12.2	4.99	232	27.05	179	42.58
A	5	ARC-6	1259	13.15	19.4	5.59	12.5	3.21	453	22.02	358	24.23
E	5	HAB-3	1415	20.61	20.7	7.82	11.7	5.38	918	13.73	840	12.56
E	5	HAB-6	1077	32.4	21.3	7.65	11.7	3.77	566	18.73	479	18.37
E	5	HUA-4	1234	15.36	19.3	2.65	12.4	7.72	247	32.79	194	34.54
E	5	HUA-6	1477	19.77	19.3	3.66	12.6	3.35	304	8.22	215	7.44
J	5	JUG-3	1510	9.3	18.4	3.41	10.2	3.23	1,099	18.15	737	23.0
J	5	OCH-3	1734	6.31	19.2	3.69	11.7	4.15	860	6.89	867	14.95
E	6	HAB-1	629	51.55	24.2	3.79	10.9	2.06	1708	9.69	1549	8.78
J	6	JUG-1	1515	10.73	19.7	5.06	9.6	6.74	2274	9.8	1363	6.64
J	6	JUG-15	2275	9.78	15.4	8.23	9.1	7.35	1941	27.79	1183	8.54
J	6	JUG-2	1325	8.42	19.6	3.03	8.6	2.76	2087	8.53	1189	3.36
J	6	JUG-9	1933	12.78	16.6	6.31	9.0	5.15	1456	18.37	1148	3.53
J	6	OCH-1	1472	10.09	19.9	4.57	9.9	5.47	2009	10.63	1333	12.87
L	6	PIM-1	379	41.56	25.5	3.5	10.4	6.78	2080	20.82	1655	15.38
L	6	PIM-2	289	60.14	24.3	3.52	8.2	1.62	2494	17.3	1221	5.2

Table 4. Medians comparisons of the informative variables that integrate the first three principal components for the 6 clusters formed in the CA of the wild tomato species in Latin America. EVAPO = Annual evapotranspiration, BIO12 = annual precipitation, BIO13 = precipitation of wettest month, ALT = altitude, BIO8 = mean temperature of wettest quarter, BIO5 = maximum temperature of warmest month, BIO2 = mean diurnal range, BIO1 = annual mean temperature, BIO15 = precipitation seasonality, and BIO3 = isothermality.

	CP1				CP2				CP3	
	EVAPO	BIO12	BIO13	ALT	BIO8	BIO5	BIO2	BIO1	BIO15	BIO3
1	137 d	194 d	69 c	2526 b	14.0 cd	20.5 d	12.6 b	12.8 d	127 a	74.6 c
2	389 c	262 d	54 c	155 d	25.1 a	30.0 a	9.0 e	22.7 a	89 b	67.7 d
3	521 c	628 c	117 b	2562 ab	16.5 c	24.0 c	13.7 a	16.4 c	80 c	84.1 b
4	805 b	962 b	141 b	2675 a	13.9 d	20.7 d	10.9 d	13.8 cd	43 d	85.0 ab
5	508 c	630 c	129 b	1431 c	20.3 b	26.0 b	11.9 c	19.3 b	92 bc	86.6 a
6	1277 a	2044 a	253 a	1398 c	19.8 b	25.4 b	9.3 e	19.7 ab	35 d	88.9 a

Medians with the same letter within each column are not statistically different ($p \leq 0.05$) according to the multiple comparisons and Kruskal–Wallis test.

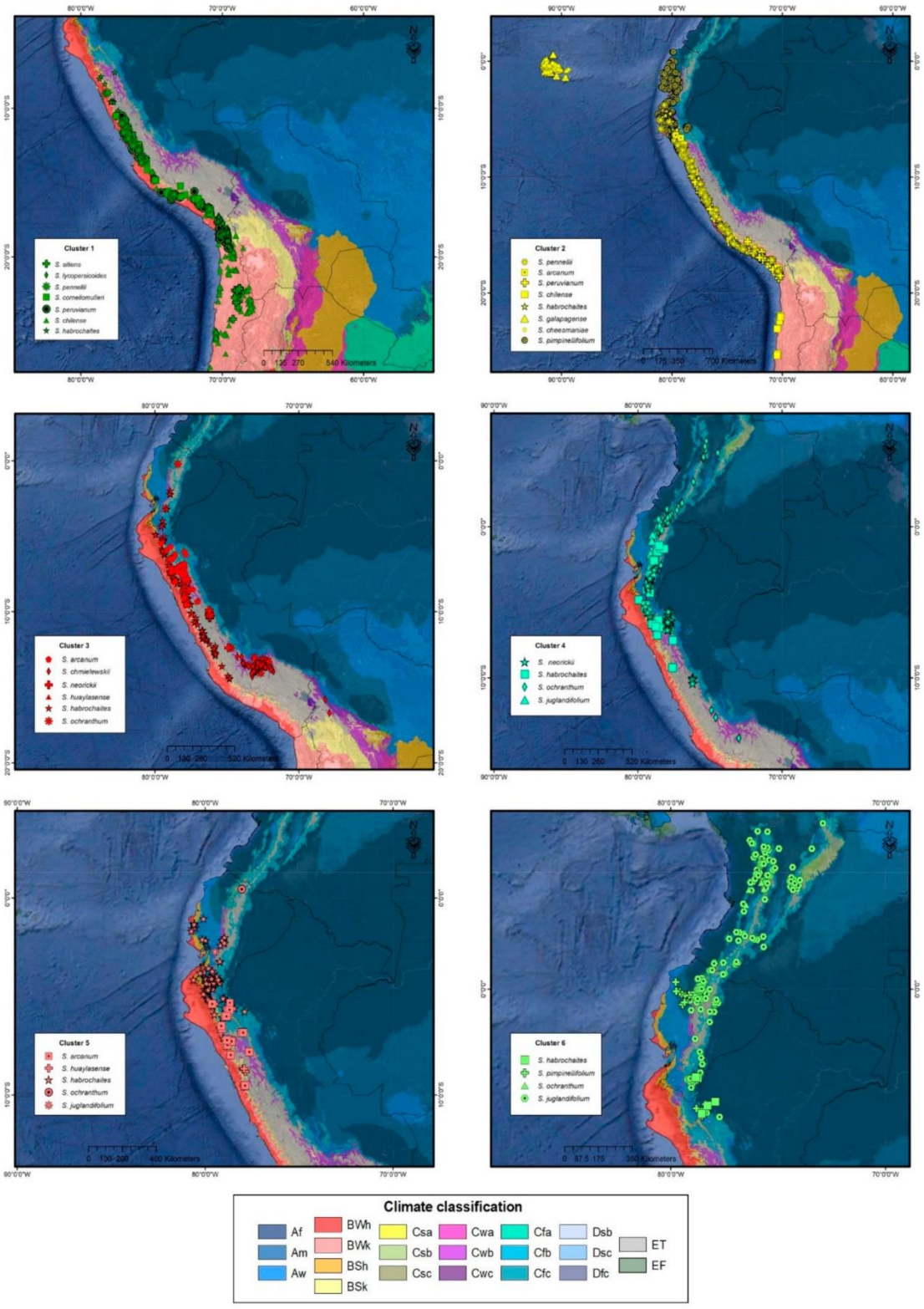

Figure 4. Clusters formed and their distribution of 12 wild tomatoes and 4 related species of *S. lycopersicum* based on climatic variables using Gower's distances and Ward's grouping method.

3. Discussion

Characterization of genetic resources through environmental information of accession sites, also called ecogeographic description, allows the typification of adaptive ranges and the most relevant environmental factors that determine species adaptation [24]. On the other hand, using GIS techniques, georeferencing species sites allows the analysis of geographical distances and distribution patterns of germplasm collection sites. With this approach, it is possible to determine environmental conditions in which the wild species and local varieties of crops have acquired their adaptive ranges [25]. This ecogeographic characterization complements the phenotypic and genetic information, useful for the characterization of the germplasm.

The distribution of the 67 combinations of species with climates in the clusters and the phylogenetic group to which they belong can be observed in Table 3. The Lycopersicon group, corresponding to the species of the Galapagos Islands and some continental areas, is located in clusters 2 and 6. *S. pennelli* (Neolicopersicon group) is located in clusters 1 and 2. The species of the Arcanum group and *S.* sect. *Juglandifolia* are located in four of the six proposed clusters. *S. huaylasense*, *S. corneliomulleri*, *S. peruvianum*, *S. chilense*, and *S. habrochaites*, species of the Ericopersicon group are distributed in all the clusters formed. On the other hand, *S.* sect. *Lycopersicoides* is only present in cluster 1.

Some species are distributed in a more restricted area (*S. lycopersicoides*, *S. sitiens*), and others are more widely located, a condition attributed to their wide distribution. It is worth mentioning that each species has a specific geographic distribution, with overlapping regions between various species, reflecting their ecological adaptation patterns and habitat preferences [22] (Figure 2).

Regarding the climatic diversity of the species of the genus *Solanum*, there were no concrete data in the literature for all the species considered within the tomato group. Thus, the diversity of climates, ecological descriptors, and abundance patterns described by this research for each species constitutes new and valuable information, with potential use for the identification of germplasm tolerant to specific adverse biotic and abiotic factors, among other purposes (Tables 2–4, Figures 2 and 3). Wild tomato species are frequently found in isolated valleys with adaptations to particular types of climate, with possible tolerance or resistance to adverse conditions. Probably the Andean geography, the ecological diversity of habitats and climates together contributed to the diversity of wild species [32,33]. In general, it is mentioned that the wild tomato species are distributed in Ecuador, the Galapagos Islands, Peru, and the north of Chile and Colombia, in various ecosystems from sea level to approximately 3300 m above sea level [33–35]. It is important to highlight that a predictive classification of tomatoes and closely related groups were considered as a framework for the ecogeographic characterization and the actual taxonomic knowledge to select reliable species accessions from different sources of the database. This selection process is fundamental to generate a trustworthy species database for further analysis. There are often mistakes and inconsistencies due to incorrect taxonomic identification of accessions or wrong information of collection sites.

Few studies have been carried out with an ecogeographic or climatic approach, highlighting the publications of Peralta et al. [1], Nakazato et al. [22], Grandillo et al. [23], and Pease et al. [7]. These authors identified the ecological distribution environments and altitudinal ranges of adaptation of the tomato species. Both the ecological descriptors and the patterns of climatic diversity were generated from more current and more representative sources of information due to the diversity of variables of the EIS used and a large number of accessions from different sources of information. It should be noted that, although the results in altitude and ecological zones of distribution are very similar, the ecological descriptors provide information for the 16 species with greater amplitude and precision (Tables 2 and 3).

With the information generated, it is also possible to begin to identify those species found in critical environments that can be potentially used as a source of germplasm

for genetic breeding programs for resistance to drought [11], extreme temperatures [12], resistance to pests and diseases [13,14], to mention some examples.

There are specific studies of some species to which a certain adaptation or tolerance characteristic has been attributed due to their distribution; For example, *S. pennellii* is considered a species with extreme tolerance to drought attributed to strict control of transpiration, increased efficient use of water, and tolerance to soil salinity [36,37]; *S. sitiens* is considered the species that inhabits the most arid places [38] with the ability to tolerate high levels of salinity [22], *S. habrochaites* is known to have good growth at low temperatures [39–41], and *S. lycopersicoides* has resistance to drought and has a preference for colder sites [42,43]. These statements coincide with the values obtained in the ecological descriptors; for example, *S. sitiens* and *S. lycopersicoides* are located as the species from sites with the lowest availability of humidity.

In the present study, the use of multivariate analysis allowed to satisfactorily identify the climatic variables with the greatest association with the distribution of the ecogeographic diversity of the species. The present results, through the PCA, indicated associations among variables of altitude, humidity, and temperature, explaining in good proportion the variability of the data. Such behavior in the results satisfactorily summarizes the importance of the variables in the distribution of the *Solanum* species evaluated.

The characterization of the species generated from the CA could be satisfactorily validated by means of a discriminating analysis. In addition, some of the species that form the groups agree with the analysis of morphological and genetic characters, so it is possible to assume that there are relationships between these characters and the climatic characteristics generated, coinciding with the results of previous research [1].

An example of the validation of groups mentioned above is shown between *S. sitiens* and *S. lycopersicoides* considered as a group of related species or sister taxa by a cladistic study carried out by Peralta and Spooner [3] with morphological data and other similar investigations [1,44–46]. *S. neorickii* and *S. chmielewskii* are considered sister species [1], according to studies based on ITS sequences [47], analysis of phenotypic data and microsatellite markers [48], and cladistic studies with morphological data [49].

Conesa et al. [50] performed a climatic classification of 14 of the wild and related species to *S. lycopersicum* based on the mean value of annual precipitation and temperature and the De Martonne index. These authors proposed the formation of three groups: species from humid regions (*S. ochranthum*, *S. neorickii*, *S. chmielewskii*, *S. juglandifollium* and *S. lycopersicum*), species from semi-arid sites (*S. arcanum*, *S. habrochaites*, *S. pimpinelifollium*, *S. galapagense*, and *S. chesmaniae*) and species from arid regions (*S. sitiens*, *S. chilense*, *S. lycopersicoides*, *S. penneellii*, and *S. peruvianum*). This classification agrees with the results obtained from the mean annual precipitation reported in the ecological descriptors (Table 2).

The present study, in addition to identifying valuable ecogeographic information not previously reported in the literature, constitutes a precedent for investigating from the use of tools developed by GIS, collections and/or valuable distribution areas as a source of germplasm for the development of varieties tolerant and resistant to specific biotic and abiotic factors through genetic improvement.

In addition, this information can be used for the formation of germplasm conservation strategies, identification of material in danger of extinction due to climate change, and germplasm collection routes for the formation of core collections. Likewise, when addressing the classification of the ecogeographic conditions achieved, they could be associated with the presence of adverse factors, both biotic and abiotic, to define areas with the probable presence of genes for resistance to such factors. Finally, it is important to mention that it is necessary to identify the actual and future ecological niches of the studied species, in that sense, these results constitute the first step on the ecogeography of the wild tomato species, being necessary to identify the ecological niches and the impact of climate change on their distribution and ecological patterns.

4. Materials and Methods

4.1. Database

Passport data of georeferenced accessions of 12 species of wild tomatoes (*S.* sect. *Lycopersicon*) and 4 species of phylogenetically related groups (*S.* sect. *Juglandifolia* and *S.* sect. *Lycopersicoides*) were used. A database was built with information from scientific reports and articles [36,51–55] and national (World Biodiversity Information Network) [56] and international plant inventories (Tomato Genetics Resource Center, Global Biodiversity Information Facility, Solanaceae source) [21,57,58].

It was possible to collect the coordinates of 11,707 accessions, which were reviewed to rule out atypical data, eliminating repeated records, with coordinates of little geographic precision (less than 3 decimal places) and accessions outside the study area according to altitude reported and respecting the previously distributed areas described by Peralta et al. [1] and Grandillo et al. [23] (Table 1). All these strategies were applied to avoid considering accessions that correspond to introductions outside the natural areas of distribution. Finally, a frequency analysis was applied, eliminating those accessions associated with climatic types with less than 3 accessions. From this, 4228 accessions of 12 wild tomatoes and 4 closely related species distributed in Latin America were selected (Figure 1).

4.2. Environmental Information

The EIS was built with 21 variables included annual evapotranspiration (EVAPO, mm) and site altitude (ALT, m), as well as the bioclimatic variables from WorldClim version 2.1 (1970–2000) with spatial resolution of ~1 km^2 [59]: annual mean temperature (BIO1, °C), mean diurnal range (BIO2, °C), isothermality (BIO3), seasonal temperature (BIO4), maximum temperature of warmest month (BIO5, °C), minimum temperature of coldest month (BIO6, °C), temperature annual range (BIO7, °C), mean temperature of wettest quarter (BIO8, °C), mean temperature of driest quarter (BIO9, °C), mean temperature of warmest quarter (BIO10, °C), mean temperature of coldest quarter (BIO11, °C), annual precipitation (BIO12, mm), precipitation of wettest month (BIO13, mm), precipitation of driest month (BIO14, mm), precipitation seasonality (BIO15), precipitation of wettest quarter (BIO16, mm), precipitation of driest quarter (BIO17, mm), precipitation of warmest quarter (BIO18, mm) and precipitation of coldest quarter (BIO19, mm).

Annual evapotranspiration was calculated from monthly values in raster format with a spatial resolution of 30 arcs second (~1 km^2) [60]. Finally, the altitude of the collection site of each accession was determined from an elevation model in raster format, also with spatial resolution ~1 km^2 [61].

Climatic types of the accession sites were defined from the world climatic classification with the Köppen–Geiger system [62] with a spatial resolution of ~1 km^2 proposed by Beck et al. [31]: Af, Am, Aw, BWh, BWk, BSh, BSk, Csa, Csb, Csc, Cwa, Cwb, Cwc, Dsa, Dsb, Dsc, Dsd, Dwa, Dwb, Dwc, Dwd, Dfa, Dfb, Dfc, Dfd, ET, and EF.

4.3. Climatic Diversity and Ecological Descriptors

Climatic diversity patterns were identified with vectors of the geographical location of each accession. With these vectors and the "Extraction" module of the ArcGis software "Spatial Analyst Tools", the value of each pixel of the corresponding climatic classification was considered, then all the information was integrated into a worksheet (Microsoft Excel) to identify all types and frequencies of climates for each species.

Ecological descriptors were determined with the methodology proposed by Ruiz-Corral et al. [11], using geographic location vectors of all accessions and the EIS; with this, climatic ranges of adaptation were identified. These values were obtained with the ArcGis "Spatial Analyst Tools". Information was concentrated in a worksheet where extreme (minimum and maximum) and median and coefficient of variation of each variable for each species were subsequently determined [10,27].

4.4. Statistical Analysis

Linear correlations between pairs were obtained to identify multicollinearity between variables. In those variables with an absolute coefficient greater than 0.95, one of the corresponding pairs was chosen. With the chosen variables, a PCA was carried out to identify the most important variables in the description of the variation between accessions. In order to identify the similarity between the species from the present climatic diversity, a grouping analysis (CA) was carried out with the Gower distances and Ward's method of minimum variance. In order to carry out this analysis, the possible combinations between species (16) and climatic type (11) were identified, with which 67 combinations were obtained. To corroborate the belonging observations to each identified group, a discriminant analysis was carried out. Finally, the non-parametric test Kruskal–Wallis and range comparison test [63] were performed for clusters generated. To describe the groups, the variables identified as significant in the PCA were used. Statistical analyses were carried out using the Statistical Analysis System software version 9.4 [64].

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Edaphoclimatic Descriptors of Wild Tomato Species (*Solanum* Sect. Lycopersicon) and Closely Related Species (*Solanum* Sect. Juglandifolia and Sect. Lycopersicoides) in South America

Gabriela Ramírez-Ojeda[1], *Iris Edith Peralta*[2,3], *Eduardo Rodríguez-Guzmán*[4], *Jaime Sahagún-Castellanos*[1], *José Luis Chávez-Servia*[5], *Tulio Cecilio Medina-Hinostroza*[6], *Jorge Rodrigo Rijalba-Vela*[7], *Leopoldo Pompeyo Vásquez-Núñez*[7] and *Juan Enrique Rodríguez-Pérez*[1]*

[1]Crop Science Department, Horticulture Institute, Chapingo Autonomous University (UACh), Chapingo, Mexico, [2]Agronomy Department, Agricultural Sciences Faculty, National University of Cuyo (UNCUYO), Mendoza, Argentina, [3]Scientific Technological Center CONICET, Argentine Institute for Arid Zones Research, Mendoza, Argentina, [4]Agronomy Department, University Center for Biological and Agricultural Sciences, University of Guadalajara (UdG), Zapopan, Mexico, [5]Interdisciplinary Research Center for Integral Regional Development Oaxaca Unit, National Polytechnic Institute (IPN), Oaxaca, Mexico, [6]Directorate of Genetic Resources and Biosafety, Ministry of Environment, Lima, Peru, [7]Biological Sciences Faculty, National University Pedro Ruiz Gallo (UNPRG), Lambayeque, Peru

Wild species related to cultivated tomato are essential genetic resources in breeding programs focused on food security to face future challenges. The ecogeographic analysis allows identifying the species adaptive ranges and most relevant environmental variables explaining their patterns of actual distribution. The objective of this research was to identify the diversity, ecological descriptors, and statistical relationship of 35 edaphoclimatic variables (20 climatic, 1 geographic and 14 edaphic variables) from 4,649 accessions of 12 wild tomato species and 4 closely related species classified in *Solanum* sect. Lycopersicon and clustered into four phylogenetic groups, namely "Lycopersicon group" (*S. pimpinellifolium*, *S. cheesmaniae*, and *S. galapagense*), "Arcanum group" (*S. arcanum*, *S. chmielewskii*, and *S. neorickii*), "Eriopersicon group" (*S. habrochaites*, *S. huaylasense*, *S. corneliomulleri*, *S. peruvianum*, and *S. chilense*), "Neolycopersicon group" (*S. pennellii*); and two phylogenetically related groups in *Solanum* sect. Juglandifolia (*S. juglandifolium* and *S. ochranthum*), and section Lycopersicoides (*S. lycopersicoides* and *S. sitiens*). The relationship between the climate and edaphic variables were determined by the canonical correlation analysis, reaching 89.2% of variation with the first three canonical correlations. The most significant climatic variables were related to humidity (annual evapotranspiration, annual precipitation, and precipitation of driest month) and physicochemical soil characteristics (bulk density, pH, and base saturation percentage). In all groups, ecological descriptors and diversity patterns were consistent with previous reports. Regarding edaphoclimatic diversity, 12 climate types and 17 soil units were identified

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Muhammad Azhar Nadeem, Sivas University of Science and Technology, Turkey

***Correspondence:**
Juan Enrique Rodríguez-Pérez
erodriguezx@yahoo.com.mx

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among all species. This approach has promissory applications for biodiversity conservation and uses valuable genetic resources related to a leading crop.

Keywords: wild tomatoes, edaphoclimatic diversity, ecological descriptors, genetic resources, canonical correlation analysis

INTRODUCTION

Latin America and the Caribbean are regions rich in biodiversity, hosting nearly 60% of the world's biological diversity (UNEP-WCMC, 2016). Within this region, Mesoamerica is recognized as one of the main centers of origin, diversification, domestication, and biological plant diversity of various species of agricultural interest and animal consumption (Fortuny-Fernández et al., 2017). The complex evolutionary history, phylogenetics, geology, biogeography, and climatic variability are some factors that enhance the diversity in this area (UNEP-WCMC, 2016). This condition is essential to ensure food, socioeconomic, and cultural sovereignty for sustainable development and offers a large number of ecosystem services (FAO et al., 2019).

In this sense, tomato (*Solanum lycopersicum* L.) is one of the most cultivated vegetables due to its wide distribution and environmental adaptation in warm, subtropical, and tropical regions with nutritional and commercial importance worldwide (Peralta et al., 2008; Ramírez-Ojeda et al., 2021a). Regarding the place of origin and diversification of tomato, Peru is considered the center of origin with two transitions that involve tomato diversification process; the first one in South America, from wild species *S. pimpinellifolium* L. to a partially domesticated species *S. lycopersicum* L. var. *cerasiforme* (SLC); the second transition occurred in Mesoamerica from SLC to the completely domesticated species *S. lycopersicum* L. var. *lycopersicum*. However, new findings indicate that the origin of SLC may be prior to its domestication since many typical characteristics of tomatoes grown in South America come from this species; SLC is subsequently considered to have been lost or declined once the partially domesticated forms extended to the north (Razifard et al., 2020).

Wild species related to cultivated tomatoes are essential genetic resources in breeding programs focused on food security to face future challenges. Therefore, it is of strategic importance to study the climatic and edaphic factors that help to understand their current distribution patterns, as well as to establish the best indicators predicting possible effects of climate change and natural or anthropic environmental alterations. This is why it is necessary to undertake national and regional strategies for the conservation and use of cultivated and wild tomato genetic resources (Sandoval-Ceballos et al., 2021).

Based on an integrative taxonomy, which includes multiple evidences, the classification of wild tomatoes and their wild relatives was proposed: *Solanum* section Lycopersicon (Mill.) Wettst. comprises cultivated tomato (*S. lycopersicum* L.) and 12 wild tomato species: *S. arcanum* Peralta, *S. cheesmaniae* (L. Riley) Fosberg, *S. chilense* Dunal, *S. chmielewskii* (C. M. Rick, Kesicki, Fobes, and M. Holle), D. M. Spooner, G. J. Anderson, and R.K. Jansen, *S. corneliomulleri* J. F. Macbride, *S. galapagense* S. C. Darwin and Peralta, *S. habrochaites* S. Knapp and D. M. Spooner, *S. huaylasense* Peralta, *S. neorickii* D. M. Spooner, G. J. Anderson and R. K. Jansen, *S. pennellii* Correll, *S. peruvianum* L., and *S. pimpinellifolium* L. Four phylogenetically related *Solanum* species are also considered in the present study: *S. juglandifolium* Dunal, *S. ochranthum* Dunal (*Solanum* sect. Juglandifolia (Rydb.) A. Child), *S. lycopersicoides* Dunal, and *S. sitiens* I. M. Johnston (*Solanum* section *Lycopersicoides* (A. Child) Peralta) (Peralta et al., 2008; Causse et al., 2016; Tropicos.org, 2021).

Evidence of phylogenetic relationships of these species have been studied in detail by Peralta et al. (2008), who have proposed a six-group classification of wild tomatoes and phylogenetically closely related species: Section Lycopersicon: "Lycopersicon group" (*S. pimpinellifolium*, *S. cheesmaniae*, and *S. galapagense*), "Arcanum group" (*S. arcanum*, *S. chmielewskii*, and *S. neorickii*), "Eriopersicon group" (*S. habrochaites*, *S. huaylasense*, *S. corneliomulleri*, *S. peruvianum*, and *S. chilense*), "Neolycopersicon group" (*S. pennellii*); and two outgroups: Section Juglandifolia (*S. juglandifolium* and *S. ochranthum*) and Section Lycopersicoides (*S. lycopersicoides* and *S. sitiens*). This classification has been verified by molecular, genomic, and transcriptomic evidence of wild tomatoes (Rodríguez et al., 2009; Aflitos et al., 2014; Pease et al., 2016) and recently has been used for ecogeographic studies with satisfactory results (Ramírez-Ojeda et al., 2021a).

By considering plant genetic resources as the biological foundation for maintaining and improving crop productivity (Kantar et al., 2015), wild tomato species constitute an important gene pool due to the presence of genes with tolerance and resistance to biotic and abiotic factors (Arellano-Rodríguez et al., 2013; Cervantes-Moreno et al., 2014; Nosenko et al., 2016; Razali et al., 2018; Dinh et al., 2019) with potential use for breeding programs. Additionally, several questions arise about these gene pools, such as current distribution, population dynamics *in situ* or *ex situ*, and how are they used directly or as sources of genes to generate new varieties that respond to current and future basic problems of tomato cultivation (for example, climate change, diseases, pests), including the contribution of genes capable of conferring a greater nutritional–nutraceutical quality to new varieties (Chávez-Servia et al., 2011; Hernández-Bautista et al., 2014).

Identification of variables that derive in adaptation and speciation processes requires a large amount of field data of significant variables in natural populations. Recent developments and the use of remote sensing technologies, as well as a great availability of environmental information derived from Geographic information systems (GIS), have made it possible

to identify patterns of species environmental variations at different scales (Nakazato et al., 2010). These tools and the availability of databases, with passport information of specimens collected in natural areas, allow for verification of the presence of species in a geographic range, as well as possible ecological descriptors, that is, to describe in detail the environmental conditions associated with the distribution of natural populations (Nakazato et al., 2010; Sánchez-González et al., 2018; Vilchez et al., 2019; Ministerio del Ambiente, 2020; Ramírez-Ojeda et al., 2021a).

One way to identify the adaptive ranges and most relevant variables that determine species distribution of valuable genetic resources is through ecogeographic studies, focusing on collection, conservation, characterization, documentation, and use of these resources (Parra-Quinajo et al., 2012; Pease et al., 2016), with the purpose of describing and explaining spatial patterns and processes involved in biodiversity distribution through time and space (Martiny et al., 2006; Tofalo et al., 2013; Délices et al., 2019). Ecogeographic studies of plant genetic resources allow the identification of the adaptive ranges of the species and the most relevant environmental variables that define their distribution (Parra-Quinajo et al., 2012; Ramírez-Ojeda et al., 2021a). Through ecogeographic studies, it is also possible to predict the environmental characteristics of the accession sites (Steiner and Greene, 1996) from ecological descriptors obtained through GIS tools using the geographical location and environmental variables (Lobo-Burle et al., 2013; Sánchez-González et al., 2018; Ramírez-Ojeda et al., 2021a, 2021b).

Currently, several information sources about geographical distribution of tomato species can be found in public databases (GBIF, 2021; Solanaceae Source, 2021; TGRC, 2021), conservation programs and gene banks (Córdoba-Téllez and Molia-Moreno, 2006; Florido et al., 2009; Magallanes-López et al., 2020), and genetic resources baseline studies (Ministerio del Ambiente, 2020), as well as some studies on geographic distribution patterns and ecological and climatic descriptors of wild tomato species (Peralta et al., 2008; Chetelat et al., 2009; Nakazato et al., 2010; Grandillo et al., 2011; Gonzá lez et al., 2013; Vilchez et al., 2019; Ramírez-Ojeda et al., 2021a). However, information regarding edaphic conditions of the sites where these species are located is limited or unknown (Balaguera-López et al., 2009).

Soil, a finite and nonrenewable natural resource, is of great importance in a large number of environmental services such as food and biomass production, climate regulation, carbon fixation, water storage and filtration, biogeochemical cycles, biodiversity reserve, and human physical and cultural environment (Burbano-Orjuela, 2016). Therefore, when considering edaphic together with climatic characteristics, it allows having a better understanding of the ecological and distribution patterns of the species.

Due to the limited edaphic information available regarding optimal characteristics for development of wild tomato species, the aim of the present work was to study ecological descriptors associated with soil characteristics and their relationship and the statistical association with climatic variables. Likewise, it was also analyzed whether the classification of wild tomatoes is related to the edaphoclimatic descriptors and supports the proposed groups of species.

MATERIALS AND METHODS

Database

Initial database consisted of 12,131 accessions of 12 wild tomato species and 4 phylogenetically related species. Of these, 7,482 accessions were eliminated due to atypical data, repeated records, or accessions with little geographic precision and outside natural areas identified according to the altitude and ecological ranges reported (Peralta et al., 2008; Grandillo et al., 2011; Ministerio del Ambiente, 2020). The final 4,649 accessions database came from scientific reports, articles (Sotomayor et al., 2019; Razifard et al., 2020), international plant repositories (Tomato Genetic Resource Center, Global Biodiversity Information Facility, Solanaceae Source) (GBIF, 2021; Solanaceae Source, 2021; TGRC, 2021), and new accessions collected in 2018–2019 in Peru (Ministerio del Ambiente, 2020). The distribution of 16 species is shown in **Figure 1**. The species distribution is shown in Figure A1 in the **Supplementary Material**. It should be noted that *S. lycopersicum* was not included because its wide distribution would not reflect a natural but artificial distribution due to anthropic dispersal as a cultivated or ruderal species.

Environmental Information

For the statistical analysis and ecological descriptors, an environmental information system with 900 m spatial resolution was built with 35 variables (**Table 1**). Nineteen bioclimatic variables were obtained from WorldClim version 2.1 from period 1970 to 2000 (Fick and Hijmans, 2017). Annual evapotranspiration (ET) was calculated from the sum of monthly values reported by Trabucco and Zomer (2019). Altitude (Alt), a geographic variable, was obtained with an elevation model from WorldClim (Fick and Hijmans, 2017). Alt was analyzed together with climatic variables due to the strong influence on the definition of climates. Finally, 14 edaphic variables obtained from the Harmonized World Soil Database version 1.1 (FAO/IIASA/ISRIC/ISSCAS/JRC, 2009) were used.

Edaphoclimatic diversity patterns were identified from climate types corresponding to world climatic classification proposed by Beck et al. (2018) with the Köppen–Geiger system and soil units from the Harmonized World Soil Database (FAO/IIASA/ISRIC/ISSCAS/JRC, 2009) (**Table 2**).

Canonical Correlation Analysis and Ecological Descriptors

A selection of climatic and edaphic variables was made in order to identify a strong linear dependence (collinearity) between more than two explanatory variables. For this purpose, Pearson's correlations were obtained, between variables, eliminating one

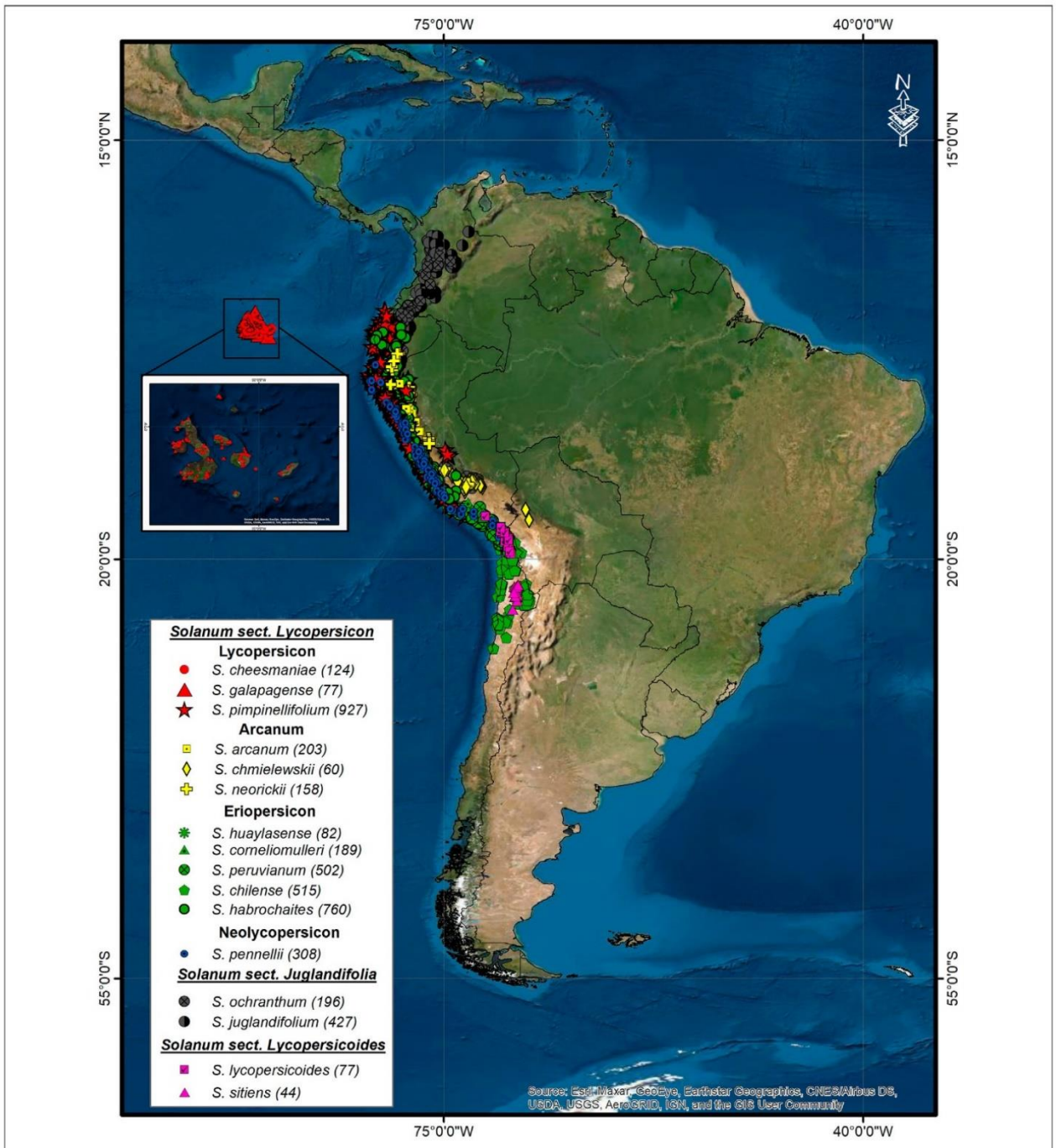

FIGURE 1 | Geographic distribution of 12 wild tomato (*Solanum* sect. Lycopersicon) and 4 closely related species (*Solanum* sect. Juglandifolia, and Lycopersicoides). In parenthesis, number of accessions after each species name.

of each pair whose absolute coefficient was greater than 0.90. The conserved variable was the one that showed the highest number of correlations with other variables, and therefore, the lowest number of non–linearly associated variables was maintained.

With the selected variables, a canonical correlation analysis was carried out to identify the relationship between the group of climatic variables and the group of edaphic variables. All statistical analyses were performed using SAS

TABLE 1 | Climatic, geographic, and edaphic variables used in the canonical correlation analysis and ecological descriptors.

Climatic variables
WorldClim variables (1970–2000): Annual mean temperature (**Bio1**, °C), mean diurnal range (**Bio2**, °C), isothermality (**Bio3**, Bio2/Bio7 × 100), temperature seasonality (**Bio4**, standard deviation × 100), maximum temperature of the warmest month (**Bio5**, °C), minimum temperature of coldest month (**Bio6**, °C), temperature annual range (**Bio7**, Bio5-Bio6), mean temperature of wettest quarter (**Bio8**, °C), mean temperature of driest quarter (**Bio9**, °C), mean temperature of warmest quarter (**Bio10**, °C), mean temperature mean of coldest quarter (**Bio11**, °C), annual precipitation (**Bio12**, mm), precipitation of wettest month (**Bio13**, mm), precipitation of driest month (**Bio14**, mm), precipitation seasonality (**Bio15**, coefficient of variation), precipitation of wettest quarter (**Bio16**, mm), precipitation of driest quarter (**Bio17**, mm), precipitation of warmest quarter (**Bio18**, mm), and precipitation of coldest quarter (**Bio19**, mm) (Fick and Hijmans, 2017). Annual evapotranspiration (**ET**, mm) (Trabucco and Zomer, 2019)
Geographic variables
Altitude (**Alt**, masl) (Fick and Hijmans, 2017)
Edaphic variables
Percentage of gravel (**GR**, %), sand (**SA**, %), silt (**SI**, %), and clay (**CL**, %), bulk density (**BD**, kg/dm^3), organic carbon (**CO**, %), **pH**, cation exchange capacity (**CEC** cmol/kg), base saturation (**BS**, %), calcium carbonate (**$CaCO_3$**, %), total exchangeable bases (**TEB**, cmol/kg), calcium sulfate (**$CaSO_4$**, %), salinity (**SAL**, dS/m), and sodium (**SOD**, %) (FAO/IIASA/ISRIC/ISSCAS/JRC, 2009)

TABLE 2 | Climate types and soil units used to determine edaphoclimatic diversity patterns.

Climate type
Af (tropical and rainforest), Am (tropical and monsoon), Aw (tropical and savannah), BWh (arid, desert, and hot), BWk (arid, desert, and cold), BSh (arid, steppe, and hot), BSk (arid, steppe, and cold), Csa (temperate, dry summer, and hot summer), Csb (temperate, dry summer, and warm summer), Csc (temperate and dry and cold summer), Cwa (temperate, dry winter, and hot summer), Cwb (temperate, dry winter, and warm summer), Cwc (temperate, dry winter, and cold summer), Cfa (temperate, no dry season, and hot summer), Cfb (temperate, no dry season, and warm summer), Cfc (temperate, no dry season, and cold summer), Dsa (cold, dry summer, and hot summer), Dsb (cold, dry summer, and warm summer), Dsc (cold, dry summer, and cold summer), Dsd (cold, dry summer, and very cold winter), Dwa (cold, dry winter, and hot summer), Dwb (cold, dry winter, and warm summer), Dwc (cold, dry winter, and cold summer), Dwd (cold, dry winter, and very cold winter), Dfa (cold, no dry season, and hot summer), Dfb (cold, no dry season, and warm summer), Dfc (cold, no dry season, and cold summer), Dfd (cold, no dry season, and very cold winter), ET (polar and tundra), and EF (polar and frost) (Beck et al., 2018)
Soil units
AC (Acrisol), **AL** (Alisol), **AN** (Andosol), **AR** (Arenosol), **AT** (Anthrosol), **CH** (Chernozem), **CL** (Calcisol), **CM** (Cambisol), **FL** (Fluvisol), **FR** (Ferralsol), **GL** (Gleysol), **GR** (Greysem), **GY** (Gypsisol), **HS** (Histosol), **KS** (Kastanozem), **LP** (Leptosol), **LV** (Luvisol), **LX** (Lixisol), **NT** (Nitisol), **PD** (Podzoluvisol), **PH** (Phaezem), **PL** (Planosol), **PT** (Plinthosol), **PZ** (Podzol), **RG** (Regosol), **SC** (Solonchak), **SN** (Solonetz), and **VR** (Vertisol) (FAO/IIASA/ISRIC/ISSCAS/JRC, 2009)

software (Statistical Analysis System) version 9.3 (SAS Institute, 2011).

Regarding ecological descriptors, these were calculated for each variable and each species (12 wild tomato and 4 phylogenetically related species) with the methodology proposed by Steiner and Greene (1996). Ecological descriptors were determined by vectors calculated with the geographic coordinates of each accession and the punctual value of each variable extracted with GIS.

Subsequently, the edaphic and climatic variables were identified as significant in the canonical correlation analysis; the extreme values (maximum and minimum), the median, and the coefficient of variation (CV = (Q/Med) × 100, where Q = (Q3 − Q1)/2 (interquartile range), and Med = median) were identified.

Finally, to identify the ecological distribution patterns of every group of species, altitude, annual mean temperature, precipitation, and annual evapotranspiration were considered as climatic variables and pH, cation exchange capacity (CEC), bulk density (BD), and base saturation (BS) as edaphic variables. These variables were chosen due to the importance and influence they have on the distribution and development of the species (Ramírez-Ojeda et al., 2021b), in addition to the importance and significance that they showed in the statistical analyses.

Edaphoclimatic Diversity

Edaphoclimatic diversity was identified using GIS tools with the vector of geographic coordinates of each accession and raster images of climate types and soil units (**Table 2**). **Figure 2** shows the distribution of climate types and soil units in South America. With the resulting information, a frequency table by climate type and soil unit was obtained for each species group (6) and for each individual species (16).

Hot spot Analysis

Critical points of species abundance and areas with the greatest diversity concentration were established using ArcGIS with the "Spatial Statistics Tools" module. Spatial density maps were constructed by adding all those accessions of each species with a distance between accessions of 1 km. A distance criterion was chosen based on previous diversity studies of potato species (*Solanum* Sect. *Petota*), the sister group of tomatoes (Hijmans et al., 2002; Spooner et al., 2010). Subsequently, hot spot spatial analysis was performed with Getis-Ord Gi* statistic (Getis and Ord, 1992) to quantify the specific areas of high clustering and spatial significance for species abundance and diversity.

The hot spot analysis determines the spatial grouping of points higher (hot spot) or lower (cold spot) than the expected by a

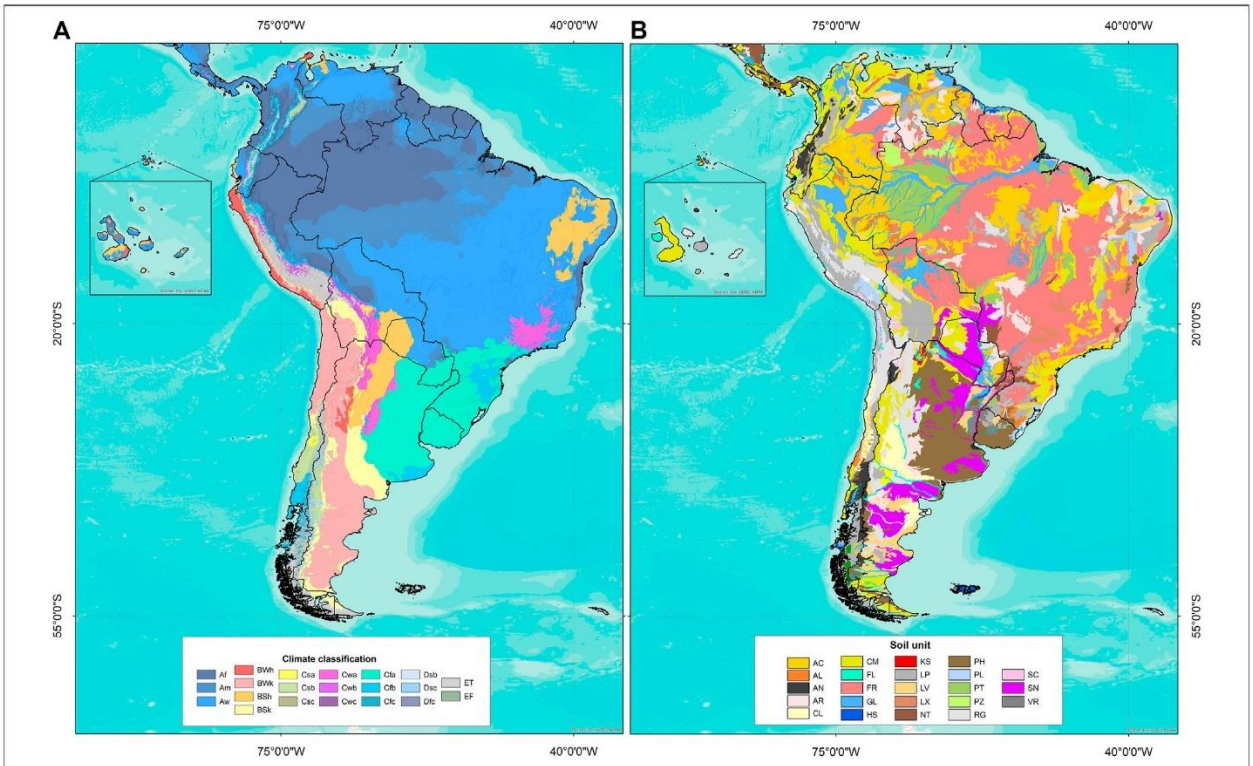

FIGURE 2 | (A) Climate classification according to Beck et al. (2018): Af (tropical and rainforest), Am (tropical and monsoon), Aw (tropical and savannah), BWh (arid, desert, and hot), BWk (arid, desert, and cold), BSh (arid, steppe, and hot), BSk (arid, steppe, and cold), Csb (temperate, dry summer, and warm summer), Cwb (temperate, dry winter, and warm summer), Cfb (temperate, no dry season, and warm summer), and ET (polar, frost). **(B)** Soil units according to FAO/IIASA/ISRIC/ISSCAS/JRC (2009): AC (acrisol), AL (alisol), AN (andosol), AR (arenosol), CL (calcisol), CM (cambisol), FL (fluvisol), FR (ferralsol), GL (gleysol), HS (histosol), KS (kastanozem), LP (leptosol), LV (luvisol), LX (lixisol), NT (nitisol), PH (phaezem), PL (planosol), PT (plinthosol), PZ (podzol), RG (regosol), SC (solonchak), SN (solonetz), VR (vertisol).

random distribution. Significance tests were calculated using z-values (Getis and Ord, 1992).

RESULTS

Canonical Correlation Analysis and Ecological Descriptors

According to Pearson's correlation coefficients, out of the 34 edaphoclimatic variables, 19 did not present collinearity. The variables selected for subsequent statistical analyses and ecological descriptors were annual evapotranspiration, altitude, precipitation of dries month, annual precipitation, temperature annual range, isothermality, mean diurnal range, annual mean temperature, percentage of sand, silt and clay, BD, pH, organic carbon, CEC, BS, calcium carbonate ($CaCO_3$), sodicity, and salinity.

The canonical correlation analysis (CCA), performed with two groups of variables (climatic and edaphic), indicated that the first three canonical correlations had values of 0.800, 0.436, and 0.415, respectively, and percentages of explanation of data variation of 71.45, 9.38, and 8.36%, respectively, with a total of 89.20%. Likelihood ratio tests indicated that the three canonical correlations are different from zero ($p \leq 0.0001$).

Correlations between climate characteristics and their canonical variables indicated that CLIMATE1 is associated with annual evapotranspiration (ET, −0.907), annual precipitation (Bio12, −0.947), and precipitation of driest month (Bio14, −0.864). The CLIMATE2 vector is associated with altitude (Alt, −0.5164) and isothermality (Bio3, −0.5642), which roughly quantifies the "hot" (low values) and "cold" (high values) regions. The CLIMATE3 vector represents the mean annual temperature (Bio1, 0.7145) and mean diurnal range (Bio2, 0.793).

Regarding correlations of soil canonical variables, the SOIL1 vector represent BD (0.801), pH (0.658), and BS percentage (BS, 0.707). High values of the SOIL2 vector identify soils with high content of sand (0.478), pH (0.552), $CaCO_3$ concentration (0.546), and low clay content (−0.427). Finally, the SOIL3 vector does not show important correlations.

The correlations between the CLIMATE vectors with the original soil variables indicate that CLIMATE1 had correlations of importance with BD (0.641), pH (0.527), CEC (−0.452), BS (0.566), and $CaCO_3$ content (0.424). CLIMA2 and

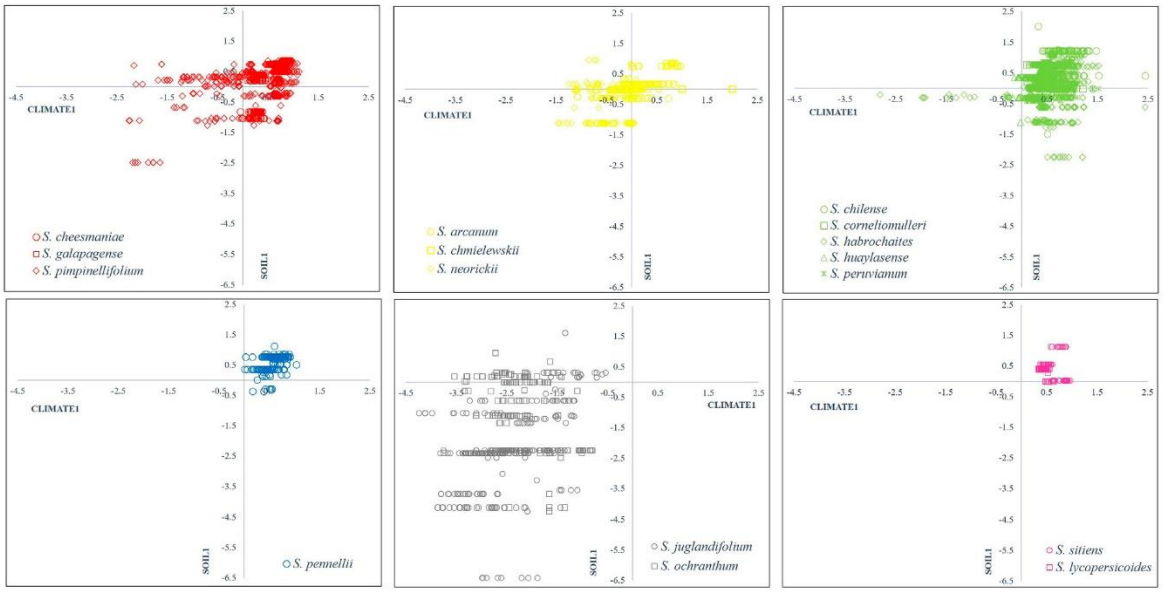

FIGURE 3 | Scatter plot of SOIL1 vs CLIMATE1 canonical vectors from CCA with 0.80 correlation and 74% of total variation. Group 1 (red): Section Lycopersicon: "Lycopersicon group", Group 2 (yellow): "Arcanum group", Group 3 (green): "Eriopersicon group", Group 4 (blue): "Neolycopersicon group" outgroup close related species in Section Juglandifolia Group 5 (grey): and Group 6 (pink): Section Lycopersicoides. In each scatter plot first-quadrant (I) represents environments with low annual evapotranspiration (ET), annual precipitation (Bio12), precipitation of driest month (Bio14) and high pH, BD, and base saturation (BS); second-quadrant (II) represents environments with high ET, Bio12, Bio14 and high pH, BD and BS; third-quadrant (III) represents environments with high ET, Bio12, Bio14 and low pH, BD and BS; fourth-quadrant (IV) represents environments with low ET, Bio12, Bio14, and low pH, BD, and BS.

CLIMA3 did not show correlation of importance. SOIL1 with climate variables showed associations with annual evapotranspiration (ET, −0.7267), annual precipitation (Bio12, −0.7585), precipitation of driest month (Bio14, −0.6924), isothermality (Bio3, 0.5404), and temperature annual range (Bio7, 0.5117). SOIL2 and SOIL3 did not show correlation of importance.

Figure 3 shows the relationship between canonical variables CLIMATE1 and SOIL1, representing 71.45% of the total data variability and a positive correlation of both canonical variables of 0.80. This figure shows the distribution and ecological adaptation of every species regarding canonical correlations.

Table 3 and **Table 4** show the ecological descriptors of edaphic and climatic variables identified as significant in the first and second canonical correlation. These results are mostly consistent with the environmental ranges previously reported in other studies. Table A1 in **Supplementary Material** shows the ecological descriptors of the rest of the variables.

Figure 4 shows the boxplots for four climatic variables for each of the six species groups, as well as the amplitude observed for each variable.

Among the main findings, it can be observed that groups 4 (*S. pennellii*) and 6 (*S. lycopersicoides* and *S. sitiens*) are ones that contain the species that distributes in environments with the lowest availability of precipitation and evapotranspiration. Considering altitude, group 1 (*S. pimpinellifolium*, *S. cheesmaniae*, and *S. galapagense*) has the lowest average altitude, while group 6 (*S. lycopersicoides* and *S. sitiens*) has the highest average altitude. Group 1 was located in environments with the highest mean annual temperature; by contrast, group 6 had the lowest average annual temperature. Groups 2, 3, and 5 remained in transition climatic conditions with the rest of the phylogenetic groups.

The analysis of four edaphic variables in **Figure 5** determines that group 5 (*S. juglandifolium* and *S. ochranthum*) has the lowest pH average. In all groups, BD was relatively constant, with similar values in all species. The mean BS in most of the groups was greater than 80%, except for group 5, with an average value around 40%. In general, soil characteristics in all groups of species were relatively similar, except for group 5 (*S. ochranthum* and *S. juglandifolium*) which presented an opposite trend.

Edaphoclimatic Diversity

The edaphoclimatic diversity found in 16 species is shown in **Figure 6** and **Figure 7**. Regarding, climate diversity, it was possible to identify 12 climate types of the 21 reported for Latin America by Beck et al. (2018).

Within the six phylogenetically related groups identified by Peralta et al. (2008) and used by Ramírez-Ojeda et al. (2021a), specific climate type patterns can be observed, with the same climate types occurring in different proportions within each group (**Figure 6**), confirming in most of the groups, the environmental distribution similarity between the species that make them up.

S. habrochaites has the greatest diversity (11 climate types), intermedium diversity (8 climate types) was found in *S. arcanum*,

TABLE 3 | Ecological descriptors of climatic and edaphic variables associated with the first canonical correlation (71.4%) for 12 species of wild tomato and 4 closely related species. Bio12 = annual precipitation, Bio14 = precipitation of driest month, pH = hydrogen ion concentration. *Range (maximum–minimum value), **median, ***coefficient of variation.

Group/Section	Species	Bio12 (mm)	Bio14 (mm)	ET (mm)	BD (kg/dm^3)	pH	BS (%)
Lycopersicon	*S. cheesmaniae*	107–562*	0–15	187–1,125	1.1–1.4	4.3–8.5	31.0–100
		277** (21.3)***	3 (66.6)	45 (41.9)	1.3 (1.1)	7.1 (15.4)	100 (34.5)
	S. galapagense	135–546	0–15	160–1,052	1.1–1.4	4.3–8.5	31.0–100
		274 (16.0)	4 (50)	531 (30.6)	1.3 (0.4)	4.9 (22.4)	32.0 (107.8)
	S. pimpinellifolium	1–2,828	0–143	1–1,710	0.3–1.5	3.2–8.5	10.0–100
		68 (146.3)	0 (0)	43 (195.9)	1.4 (6.5)	7.6 (9.2)	100 (4.5)
Arcanum	*S. arcanum*	22–1,193	0–55	11–1,094	0.3–1.5	4.6–8.5	17.0–100
		487 (44.0)	4 (137.5)	390 (43.2)	1.3 (1.5)	6.4 (13.2)	87.0 (5.1)
	S. chmielewskii	504–1,318	4–19	429–874	1.2–1.5	5.2–8.1	19.0–100
		944 (18.2)	11 (22.7)	610 (16.9)	1.2 (2.5)	8.1 (4.3)	100 (0)
	S. neorickii	426–1,366	3–68	326–1,031	0.2–1.7	4.6–8.1	17.0–100
		817 (21.2)	18.5 (45.9)	672 (13.7)	1.2 (10.2)	5.6 (26.7)	81 (44.0)
Eriopersicon	*S. huaylasense*	128–507	0–3	73–424	1.2–1.4	5.2–7.9	21.0–100
		328 (21.5)	1 (50)	238 (23.0)	1.4 (7.9)	5.6 (12.5)	38.0 (81.5)
	S. corneliomulleri	19–434	0–2	12–354	1.1–1.5	4.2–8.1	19.0–100
		205 (59.2)	0 (0)	141 (45.7)	1.4 (6.7)	5.6 (16.9)	38.0 (86.8)
	S. peruvianum	0–534	0–3	0–427	1.2–1.5	3.2–8.6	10.0–100
		25 (97.4)	0 (0)	13 (134.6)	1.3 (4.1)	7.6 (6.3)	100 (5.0)
	S. chilense	0–355	0–1	3–275	1.0–1.5	4.2–8.6	28.0–100
		29 (68.9)	0 (0)	20 (72.5)	1.3 (2.3)	7.5 (10.6)	100 (6)
	S. habrochaites	11–2,358	0–143	8–1,682	0.3–1.7	4.3–8.5	14.0–100
		605 (42.0)	3 (266.6)	535 (43.9)	1.3 (7.6)	5.7 (15.7)	87 (35.6)
Neolycopersicon	*S. pennellii*	1–404	0–3	0–289	1.2–1.5	5.1–8.5	19.0–100
		49 (94.8)	0 (0)	33 (95.8)	1.3 (4.9)	7.9 (14.5)	100 (31.0)
Juglandifolia	*S. juglandifolium*	555–3,214	1–194	413–1,648	0.3–1.9	4.1–7.7	13.0–100
		1,895 (28.7)	60 (49.1)	1,177 (10.0)	0.9 (1.0)	5.2 (1.9)	23.0 (36.9)
	S. ochranthum	507–2,358	2–131	387–1,474	0.3–1.7	3.2–8.5	10.0–100
		1,010 (11.0)	36 (43)	814 (14.1)	1.2 (11.2)	5.6 (13.3)	45.0 (67.7)
Lycopersicoides	*S. lycopersicoides*	13–215	0–0	9–182	1.3–1.4	4.7–8.1	34.0–100
		104 (50.4)	0 (0)	82 (58.5)	1.3 (1.5)	7.5 (10.6)	100 (6.5)
	S. sitiens	8–31	0–0	9–26	1.2–1.4	6.4–7.9	88.0–100
		17 (24.2)	0 (0)	21 (16.6)	1.2 (8.5)	6.5 (10.7)	88.0 (6.8)

while *S. sitiens* has the greatest climatic restriction, located only in climates BWk (arid, desert, cold). The climate type identified in most of the accession sites was associated with the 16 species was BSk (arid, steppe, and cold), and only absent in species of Lycopersicon group (*S. cheesmaniae*, *S. galapagense*, and *S. pimpinellifolium*) and in *S. juglandifolium* and *S. sitiens*. The opposite case was presented with Cwc climate (temperate, dry winter, and cold summer) present only in some areas where *S. habrochaites* was collected. *S. juglandifolium* and *S. ochranthum* share similar climatic types but were most frequently found in Cfb (temperate, no dry season, warm summer).

Diversity of soil units among wild tomato species (**Figure 7**) found 17 different soil units out of the 23 reported for Latin America in Harmonized World Soil Database from FAO/IIASA/ISRIC/ISSCAS and JRC (2009). Most frequent soils types were leptosol (LP), present in all species, regosol (except *S. huaylasense*) and less frequently acrisol (AC), present only in some *S. pimpinellifolium* accessions.

The greatest edaphic diversity was found in *S. pimpinellifolium*, with accessions in 16 of the 17 reported soil units (except VR). The opposite case was identified for species of Lycopersicoides section *S. sitiens* and *S. lycopersicoides*, with two and four soil units, respectively. Likewise in the patterns of climatic diversity described, edaphic diversity is similar within species, integrating each of the six phylogenetically related groups.

Hot spot Analysis

Areas with a high number of species and accessions were determined by hot spot analysis. **Figure 8** shows the result of hot spot analysis applied with a distance of 1 km between accessions for 4,649 accessions of 12 wild tomato and 4 phylogenetically related species. The highest concentration of species is located in two areas of Peru, one near Trujillo and Chimbote, and the second area around Lima. Likewise, a small area with high diversity is located in southern Peru and northern limit of Chile. The zone in Trujillo–Chimbote is characterized by the presence of seven species (*S. pennellii*, *S. arcanum*, *S. neorickii*, *S. huaylasense*, *S. habrochaites*, *S. pimpinellifolium*, and *S. ochranthum*). The region of high diversity around *Lima* also

TABLE 4 | Ecological descriptors of climatic and edaphic variables associated with the second canonical correlation (9.3%) for 12 species of wild tomato and 4 closely related species. Bio3 = isothermality, Sand = sand percentage, Clay = clay percentage. *Range (maximum–minimum value), **median, ***coefficient of variation.

Group/Section	Species	Alt (m)	Bio3 (°C × 100)	Sand (%)<	$CaCO_3$ (%)	Clay (%)
Lycopersicon	*S. cheesmaniae*	5–1,478*	58.3–74.8	33–60	0–3.1	3–37
		87** (152.4)***	65 (4.5)	43 (11.6)	2 (67.3)	28 (16.0)
	S. galapagense	4–868	59.1–73.9	33–60	0–3.1	3–37
		45 (240.0)	68.3 (4.9)	34 (14.7)	0 (0)	36 (12.5)
	S. pimpinellifolium	1–1,774	48.2–89.4	0–94	0–4.3	0–56
		92 (101.9)	65.6 (8.0)	44 (51.1)	2 (65)	17 (47)
Arcanum	*S. arcanum*	132–3,292	65.5–90.1	0–83	0–4.3	0–45
		1,767 (33.1)	87 (2.7)	54 (10.1)	0 (0)	17 (8.8)
	S. chmielewskii	1,803–3,195	73.6–86.6	25–63	0–2.0	14–31
		2,445 (11.3)	82.6 (2.9)	63 (12.6)	2 (17.5)	14 (14.2)
	S. neorickii	1,202–3,262	76.4–89.1	0–76	0–2.4	0–56
		2,230 (12.2)	84.5 (1.9)	63 (30.1)	0 (0)	12 (20.8)
Eriopersicon	*S. huaylasense*	978–3,304	80.7–90.2	25–67	0–3.5	10–28
		2,301 (18.8)	87.8 (1.1)	67 (31.3)	0 (0)	10 (85)
	S. corneliomulleri	1,018–3,097	64.6–87.4	25–80	0–4.0	4–32
		2,310 (17.0)	75.8 (3.9)	57 (16.6)	0 (0)	16 (43.7)
	S. peruvianum	2–3,191	40.5–87.8	25–94	0–21.6	2–32
		532, (128.0)	62.5 (15.3)	54 (21.2)	2.9 (55.1)	16 (31.2)
	S. chilense	0–3,995	41.6–87.2	30–96	0–21.6	1–32
		1,910 (57.9)	68.1 (10.1)	54 (24.0)	3.1 (59.6)	19 (31.5)
	S. habrochaites	40–3,692	50.1–91.0	0–94	0–4.3	0–46
		2,137 (30.6)	84.5 (5.1)	51 (32.3)	0 (0)	17 (44.1)
Neolycopersicon	*S. pennellii*	5–2,921	48.0–87.4	25–94	0–7.2	2–28
		831 (52.4)	68.5 (8.2)	54 (12)	2.9 (60.3)	16 (18.7)
Juglandifolia	*S. juglandifolium*	1,005–3,153	76.5–94.5	9–94	0–2.0	2–56
		2,195 (14.3)	89.2 (1.9)	40 (25)	0 (0)	13 (46.1)
	S. ochranthum	1,195–4,008	72.4–93.8	0–83	0–2.4	0–46
		2,742 (10.5)	85.8 (3.3)	60 (16.6)	0 (0)	12 (26.0)
Lycopersicoides	*S. lycopersicoides*	1,290–3,775	65.8–85.5	30–57	0–7.2	18–32
		2,960 (13.2)	73.1 (4.6)	50 (11)	3.1 (53.2)	20 (20)
	S. sitiens	2,276–3,330	67.9–71.6	43–69	0.3–7.2	12–28
		2,740 (5.7)	69.1 (1.2)	69 (8.6)	0.3 (1,150)	12 (25)

features seven species: *S. pennellii*, *S. neorickii*, *S. corneliomulleri*, *S. peruvianum*, *S. chilense*, *S. habrochaites*, and *S. pimpinellifolium*.

Finally, the region of high diversity on the border between Chile and Peru is home to five species: *S. pennellii*, *S. peruvianum*, *S. chilense*, *S. pimpinellifolium*, and *S. lycopersicoides*.

Cold spots correspond to the geographical distribution of *S. ochranthum* and *S. juglandifolium* accessions in Colombia and Ecuador, and *S. sitiens* in the northern region of Chile. The rest of the areas of distribution are insignificant according to the statistical criteria, assuming a random distribution.

DISCUSSION

This research provides a relevant ecogeographic characterization to understand the distribution patterns of wild species that complement the phenotypic and genetic information. Characterization of genetic resources through environmental characteristics associated with accession areas and use of GIS tools allows the identification of adaptive ranges and most relevant environmental factors affecting species distribution and ecological adaptation (Parra-Quinajo et al., 2012).

Likewise, through GIS and georeferenced information of species locations, it is possible to quantify geographical distances and distribution patterns of germplasm accession sites. From this perspective, it is likely to determine specific environmental conditions in which wild species and local varieties of crops have acquired their adaptive characters (Hijmans and Spooner, 2001). Therefore, the results obtained in this research constitute a source of updated and valuable information on the edaphoclimatic characteristics in which wild tomatoes and phylogenetically related species are distributed along its natural geographic range.

In general, geographical distribution of 16 wild species related to the cultivated tomato is wide, from Colombia through Peru, comprising Pacific coastal region to Chile and the Andean mountains, with an altitudinal range from sea level to 3,300 m (Peralta et al., 2008; Bergougnoux, 2014. However, within this distribution, there are overlapping areas between several species

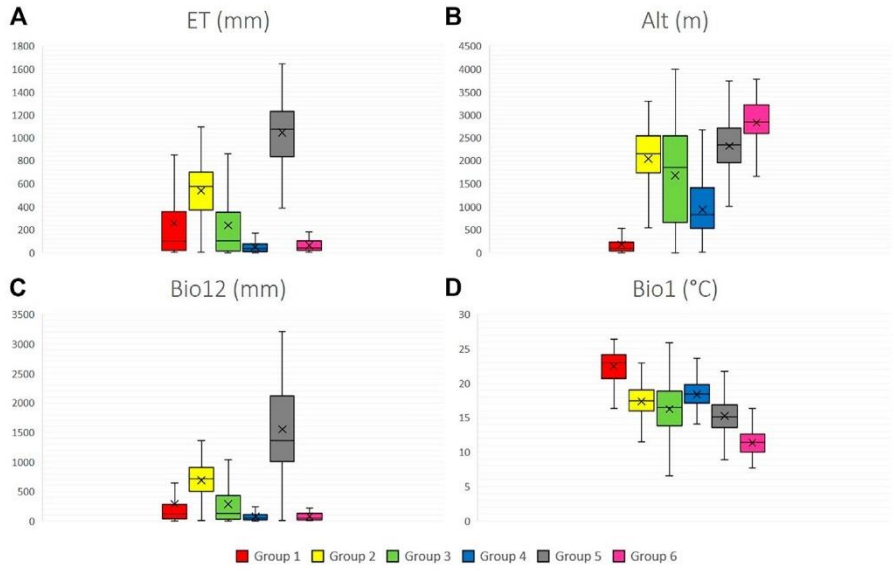

FIGURE 4 | Climate variables boxplots for six groups of 12 wild tomato species and 4 closely related species. **(A)** ET (annual evapotranspiration), **(B)** Alt (altitude), **(C)** Bio12 (annual precipitation), **(D)** Bio1 (mean annual temperature). Group 1: Section Lycopersicon: "Lycopersicon group" (*S. pimpinellifolium*, *S. cheesmaniae*, and *S. galapagense*), Group 2: "Arcanum group" (*S. arcanum*, *S. chmielewskii*, and *S. neorickii*), Group 3: "Eriopersicon group" (*S. habrochaites*, *S. huaylasense*, *S. corneliomulleri*, *S. peruvianum*, and *S. chilense*), Group 4: "Neolycopersicon group" (*S. pennellii*); outgroup close related species in section Juglandifolia Group five (*S. juglandifolium* and *S. ochranthum*) and Group six: Section Lycopersicoides (*S. lycopersicoides* and *S. sitiens*).

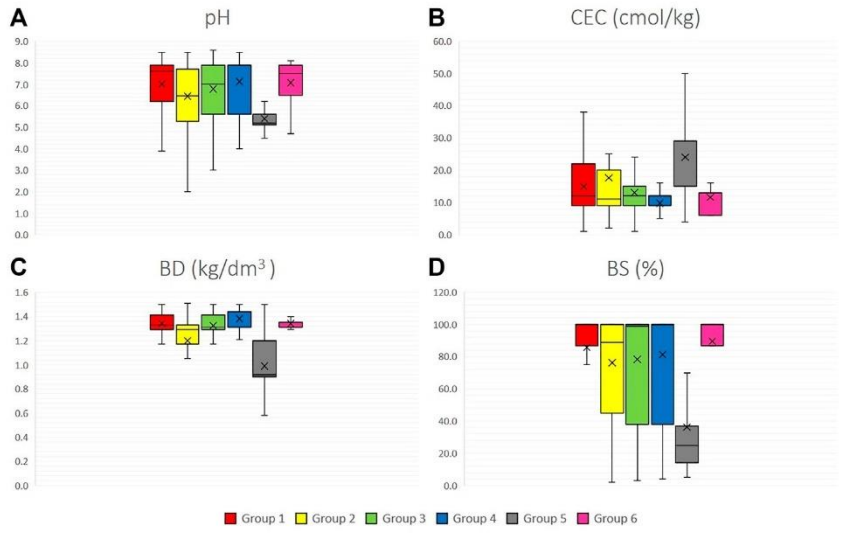

FIGURE 5 | Edaphic variables boxplots for six groups of the 12 wild tomato species and 4 related species **(A)** pH, **(B)** CEC (cation exchange capacity), **(C)** BD (bulk density), **(D)** BS (base saturation). Group 1: Section Lycopersicon: "Lycopersicon group" (*S. pimpinellifolium*, *S. cheesmaniae* and *S. galapagense*), Group 2: "Arcanum group" (*S. arcanum*, *S. chmielewskii*, and *S. neorickii*), Group 3: "Eriopersicon group" (*S. habrochaites*, *S. huaylasense*, *S. corneliomulleri*, *S. peruvianum*, and *S. chilense*), Group 4: "Neolycopersicon group" (*S. pennellii*); outgroup close related species in Section Juglandifolia Group 5 (*S. juglandifolium* and *S. ochranthum*) and Group 6: Section Lycopersicoides (*S. lycopersicoides* and *S. sitiens*).

or regions with specific distribution such as the endemic species of the Galapagos Islands (*S. cheesmaniae* and *S. galapagense*) or hyper arid regions of northern Chile with other rare endemic species, *S. sitiens*. Within these distribution patterns, it is also possible to identify differences and similarities between the species that conform each group, for example, the similarity

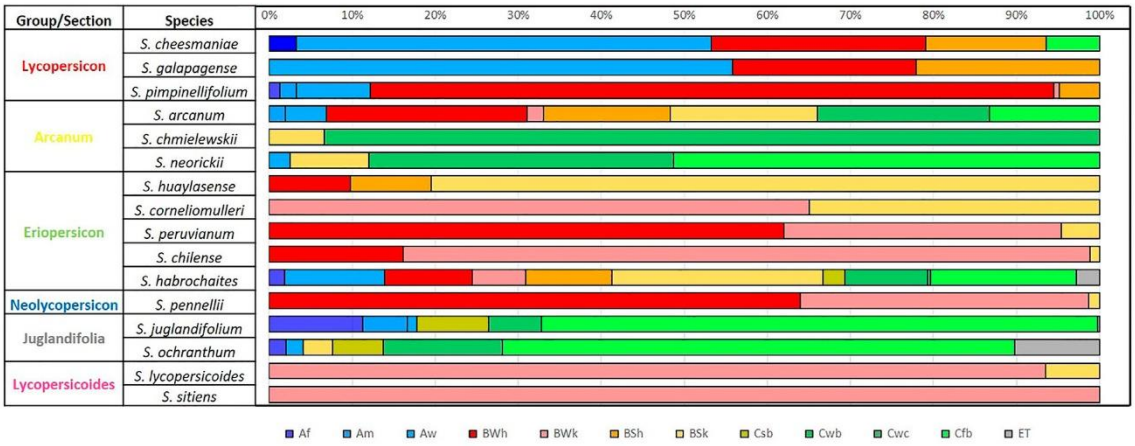

FIGURE 6 | Percentage of climate type by species according to Beck et al. (2018) of 12 wild tomato (*Solanum* Sect. Lycopersicon) and 4 closely related species (*Solanum* Sect. Juglandifolia and Sect. Lycopersicoides). Climate type: Af (tropical, rainforest), Am (tropical, monsoon), Aw (tropical, savannah), BWh (arid, desert, hot), BWk (arid, desert, cold), BSh (arid, steppe, hot), BSk (arid, steppe, cold), Csb (temperate, dry summer, and warm summer), Cwb (temperate, dry winter, and warm summer), Cfb (temperate, no dry season, and warm summer), ET (polar, frost).

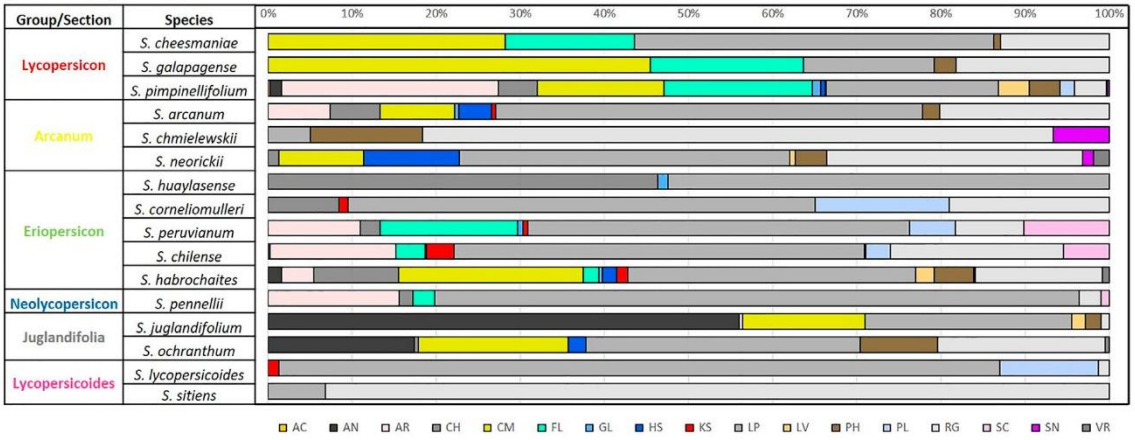

FIGURE 7 | Percentage of soil type by species according to FAO/IIASA/ISRIC/ISSCAS and JRC (2009), for 12 wild tomato (*Solanum* sect. Lycopersicon) and 4 closely related species (*Solanum* sect. Juglandifolia and sect. Lycopersicoides). Soil type: AC (acrisol), AN (andosol), AR (arenosol), CH (chernozem), CM (cambisol), FL (fluvisol), GL (gleysol), HS (histosol), KS (kastanozem), LP (leptosol), LV (luvisol), PH (phaezem), PL (planosol), RG (regosol), SC (solonchak), SN (solonetz), and VR (vertisol).

between *S. arcanum* and the species of Lycopersicon group (**Figure 6**), reflecting a wider distribution and adaptations to local sites of ecotypes (Peralta et al., 2008). These environmental characteristics reflect the ecological adaptation patterns and habitat preference of each species (Nakazato et al., 2010; Vilchez et al., 2019) (**Figures 6**, **7**, Table A1 and A3 in **Supplementary Material**). It is worth mentioning that these results also suggest a thorough revision of the proposed groups, incorporating the new passport data as well as genetic and molecular information to corroborate the belonging of each species to the phylogenetic assigned groups. The aforementioned are under the assumption that the species are closely and genetically related and in expecting that their adaptation areas are similar.

Regarding wild tomato species and phylogenetically related species, few studies have been carried out with an ecogeographic or climatic focus. A comprehensive treatment integrates main botanical, biological, and ecological characteristics of each wild tomato and related species (Peralta et al., 2008); other studies focused on distribution of species richness and diversity through the analysis with GIS (González, 2013) and established conservation priorities (Vilchez et al., 2019); further

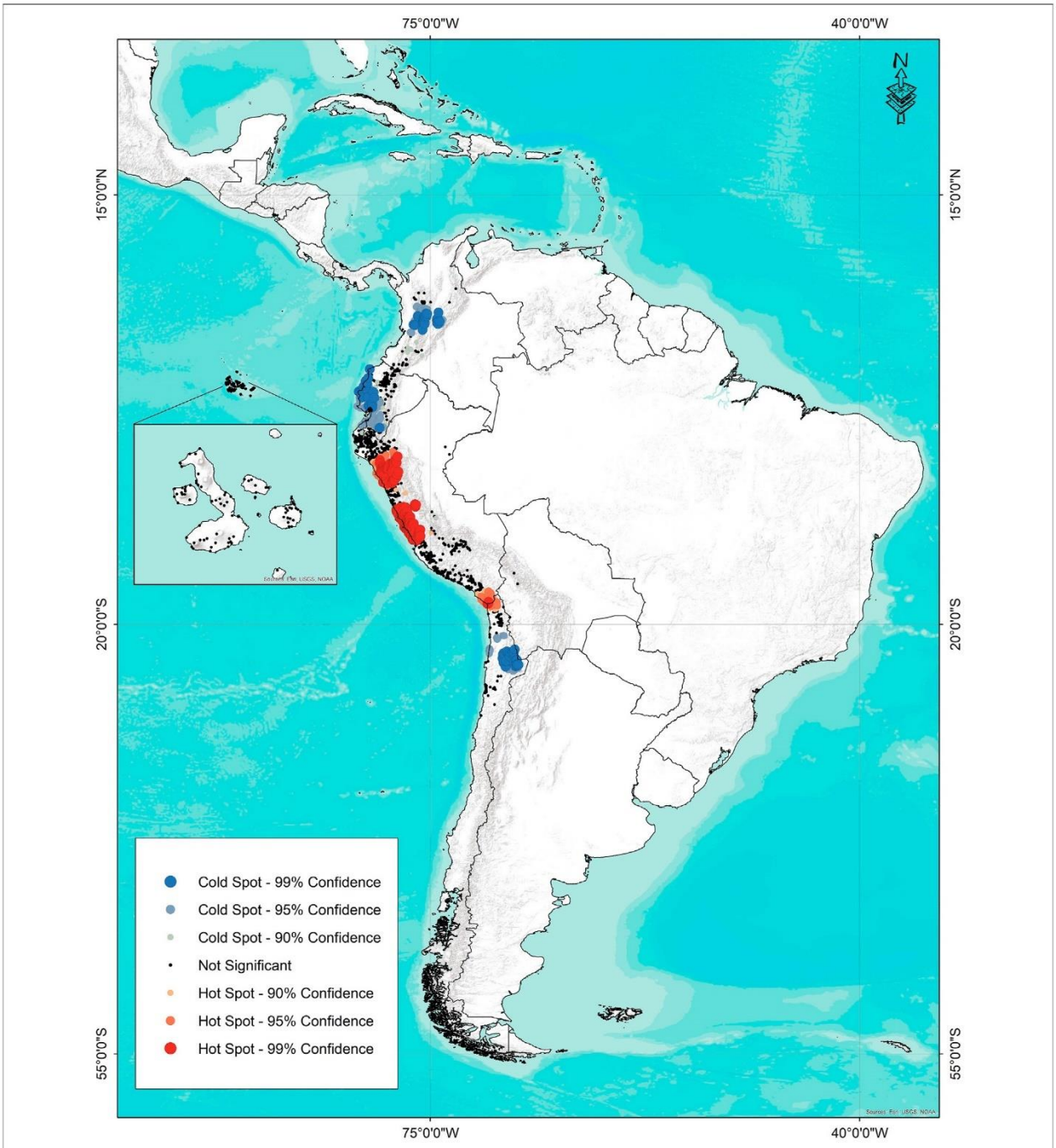

FIGURE 8 | Species diversity map hot spots (red) and cold spots (blue) for 12 wild tomato (*Solanum* Sect. Lycopersicon) and 4 closely related species (*Solanum* sect. Juglandifolia and sect. Lycopersicoides).

geographical and ecological characterization have been investigated in 10 tomato species determining soil and climate variables (Nakazato et al., 2010); studies have been conducted on tomato biogeography, *S. lycopersicum* var. *cerasiforme*, in its center of origin and domestication (Délices et al. (2019); and finally climatic effects on species distribution (Lin et al., 2020) and bioclimatic characterization, and identification of ecological descriptors and patterns of climatic diversity of 12 wild

tomato and 4 closely related species (Ramírez-Ojeda et al., 2021a) have been studied. In this sense, this study complements the information available, providing information on soil characteristics that had not been analyzed.

The canonical correlation analysis satisfactorily identifies climatic variables with greatest influence on edaphic variables and vice versa, with a correlation of 0.80 representing 74% of total variation in 4,649 accessions. One main conclusion is that variables related to water availability (ET, Bio12, Bio14) have a great influence on physical (BD) and chemical soil characteristics (BS, pH). This pattern is persistent in all six groups. This relationship can be better observed in group 5 (*S. juglandifolium* and *S. ochranthum*) accessions with greater availability of annual precipitation and evapotranspiration, which present lower pH, BD, and BS than the rest of species; that is, they are located in soils with the lowest agricultural quality (**Figures 4**, **5**). This methodological approach is promising to be applied at other scales, considering the analysis at population level of each species and climatic and edaphic factors limited to smaller areas of distribution. This basis of ecogeographic characterization could incorporate information from genetic and ecological studies. A better understanding of these variables would allow the generation of projection models in different climate change scenarios (Violle and Jiang, 2009;Luebert and Weigend, 2014; Godoy-Bürki, 2016; Lin et al., 2020).

Ecological descriptors obtained, despite the incorporation of new accessions, are very similar to the ranges reported by Peralta et al. (2008) and Ramírez-Ojeda et al. (2021a) and generally identify the groups of species proposed in the classification. It is important to mention that this methodology has been widely used in the study of other species (Ruiz-Corral et al., 2008; Cerda-Hurtado et al., 2018; Sánchez-González et al., 2018; Ramírez-Ojeda et al., 2021a; 2021b). With this information, it is also possible to identify those species with tolerance to extreme conditions, for example, low and high temperatures, humidity conditions, altitude, pH, BD, and all the possible conditions when associating a species with a climate type or soil unit (**Table 3** and **Table 4**, Tables A1, A2, and A3 in **Supplementary Material**).

Edaphic diversity (**Figure 7**) tends to be more constant between species groups and sections with respect to climate diversity. In general, considering climate and soil characteristics, specific adaptation patterns for each species group can be identified: Lycopersicon group (group 1) corresponds to species with lower altitude and higher mean annual temperature; species of Juglandifolia section (group 5) are those with the highest water availability, lowest pH, BD, and base saturation; species of Lycopersicoides section (group 6) are the ones with the highest altitude, the lowest mean annual temperature, and lowest water availability, groups 4 and 6 have the lowest water availability and soils with favorable agricultural characteristics, differing by altitude. The rest of the species (groups 2 and 3) are in the transition zones with the rest of the wild tomato species. One aspect to highlight is that when combining or considering climatic and edaphic information, it is possible to characterize in a better way the different groups, being able to better identify their differences and similarities.

Among possible uses of this approach is the identification of the germplasm with tolerance to adverse biotic and abiotic factors (Foolad and Lin., 2000; Mittova et al., 2004; Venema et al., 2005; Zhao et al., 2005; Ruiz-Corral et al., 2008; Chetelat et al., 2009; Arellano-Rodríguez et al., 2013; Ruiz-Corral et al., 2013; Cervantes-Moreno et al., 2014; Chen et al., 2015; Nosenko et al., 2016; Stam et al., 2017a; Stam et al., 2017b; Flores-Hernández et al., 2017; Razali et al., 2018; Dinh et al., 2019; Vilchez et al., 2019) with potential use for genetic breeding, identification of routes of germplasm accession, and areas of high and low diversity for use and conservation (Vilchez et al., 2019). In the information contained in **Table 3**, **Table 4**, and **Figures 4**, **5**, it is possible to identify species with extreme values that indicate tolerance or resistance to climatic and edaphic factors, with potential use as germplasm for genetic breeding.

Finally, the hot spot analysis could satisfactorily identify regions with the greatest diversity of species. These are priority areas for conservation, either due to high or low diversity. Regions identified as of great importance for conservation comprise endemism. Diversity contained in populations with few isolated individuals or with restricted distribution could be more affected by environmental and anthropic changes. This result could be explained by the quantity and geographic distance between the accessions of species studied. However, this first approximation is very useful and agrees with the diversity results obtained for wild potato species in Peru (Hijmans and Spooner, 2001).

This research determines the most important edaphoclimatic descriptors of wild tomato species and its closely related species along their natural geographic range in South America. Patterns of climatic diversity correlate with species groups and sections proposed in current classification. New edaphic characteristics analyzed in the same areas were also useful, although with less discrimination than the climatic variables. Interaction between climatic and edaphic factors allows for understanding species distribution and their adaptation patterns. Another feature to highlight is the incorporation of new data from recent collections of specimens being properly identified (Ministerio del Ambiente, 2020) that were not considered before in other studies, and thus expanding precision and reliability of these results. Most important areas for conservation of wild tomato species and related outgroups were detected. Under this premise, this contribution is promissory for further ecogeographic study of wild tomatoes and closely related species at the local population scale, especially focused *in situ* conservation reserves as well as in localities outside protected areas. Edaphoclimatic descriptors in addition with other abiotic or biotic factors could help to better estimate the species ecological niches and determine local ecotypes. Selected descriptors would be tested in models of current and future distribution considering the impact of climate change and anthropic activities along the distribution range of these valuable genetic resources.

Finally, this research can be used as a study model to replicate in other species.

DATA AVAILABILITY STATEMENT

The data sets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Solanacea source: http://solanaceaesource.org/; Tomato Genetic Resource Center: https://tgrc.ucdavis.edu; Global Biodiversity Information Facility: https://www.gbif.org.

AUTHOR CONTRIBUTIONS

Conceptualization: GR-O, IP, and JR-P; methodology: GR-O, IP, and JR-P; software: GR-O and JR-P; validation: JR-P, JS-C, ER-G, IP, JC-S, TM-H, JR-V, and LV-N; formal analysis: GR-O, JR-P, and JS-C; data curation: IP, TM-H, JR-V, and LV-N; writing—original draft preparation: GR-O, JR-P, and IP; writing—review and editing: GR-O, JR-P, JS-C, ER-G, IP, JC-S, TM-H, JR-V, and LV-N. All authors have read and agreed to the published version of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fgene.2021.748979/full#supplementary-material

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5. DISCUSIÓN GENERAL

Los recursos genéticos vegetales y animales son todas las especies, variedades, razas, líneas y genotipos en general con potencial económico, usos científicos o de interés cultural, que pueden ser usados para la producción de alimentos y/o en la agricultura (FAO, 2006).

Los recursos genéticos vegetales se conciben como la diversidad de genes contenidos en plantas que conforman la base para el desarrollo de variedades. Estas plantas son materia prima para programas de mejoramiento genético para crear variedades con mayor potencial y productividad (Agüero, 2009).

Un criterio a considerar es que la mayor parte de la producción animal y vegetal depende de pocas especies. Se estima que alrededor de 90% de los alimentos vegetales que se consumen a nivel mundial dependen de solamente 20 cultivos (FAO, 2006). Debido a lo anterior, es de suma importancia evaluar y conocer la condición actual de las especies silvestres y sus parientes cercanos, con el fin de conservar los recursos genéticos de dichos cultivos y, además, generar o diversificar nuevas alternativas de alimentación a partir de cultivos o especies poco atendidos o utilizados en forma escaza.

El tomate, considerando su demanda en el mercado mundial, es la segunda hortalizas con mayor superficie cosechada y consumo, después de la papa. En México, es la hortaliza de mayor producción para el abastecimiento de la demanda nacional y de exportación (SIAP, 2021).

México por ser centro el principal de domesticación de esta especie, es una región con gran diversidad, por lo que es posible encontrar infinidad de morfotipos con formas silvestres, cultivadas y formas con cierto grado de domesticación (Délices et al., 2019; Ranc et al., 2008; Blanca et al., 2012; Lin et al., 2014) y, además, en forma toleradas, e incluso promovidas dentro de cultivos tradicionales con bajo nivel tecnológico.

Hasta la fecha, se han realizado investigaciones sobre los recursos genéticos del tomate en aspectos relacionados con las características agro-morfológicas (Carrillo-Rodríguez et al., 2013; Contreras-Magaña et al., 2013; Bonilla-Barrientos et al., 2014; Sanjuan-Lara et al., 2014; Marín-Montes et al., 2016; Delgado-Vargas et al., 2018; Martínez-Damián et al., 2018), conservación y mejoramiento genético (Ríos-Osorio et al., 2014; Maldonado-Peralta et al., 2016; Flores-Hernández et al., 2017a; Martínez-Vázquez et al., 2017; Bonilla-Barrientos et al., 2018; Flores-Hernández et al., 2018; Carrillo-Rodríguez et al., 2019; Marín-Montes et al., 2019; Hernández-Bautista et al., 2020), calidad de fruto y postcosecha (Luna-Guevara et al., 2014; Hernández-Ibáñez et al., 2017; Tochihuitl-Martiñon et al., 2017; Martínez-Damián et al., 2019; Magallanes-López et al., 2020), resistencia a factores bióticos y abióticos (Arellano-Rodríguez et al., 2013; Leyva-Mir et al., 2013; Cervantes-Moreno et al., 2014;Sanjuan-Lara et al., 2015; Ruíz-Espinosa et al., 2014; Nieto-Ángel et al., 2019; Ledezma-Morales et al., 2020; Salinas-Vargas et al., 2020) y algunos estudios con enfoque ambiental (Rodríguez-et al., 2099; Pacheco-Triste et al., 2014; Délices et al., 2019). A pesar de ello, estos esfuerzos son pocos ante la basta variación genética de esta especie; más aún si se consideran sus parientes filogenéticos cercanos

Respecto a las especies silvestres y filogenéticamente relacionadas *a S. lycopersicum*, existen pocos o nulos estudios de carácter agronómico; en contraste, resaltan estudios resultados donde se identifican genes de tolerancia a factores ambientales como tolerancia a bajas temperaturas, sequía o salinidad (Foolad et al., 2000; Mittova et al., 2004; Zhao et al., 2005; Venema et al., 2005; Chen et al., 2015; Conesa et al., 2017).

Al referirse a los resultados de la presente investigación, constituye una base de datos actualizada y sistematizados sobre los sitios de colectas existentes de *S. lycopersicum* en México y sus parientes silvestres y emparentados filogenéticamente en Latinoamérica. Lo cual es un aporte substancial para el estudio de estos recursos fitogenéticos a nivel Latinoamérica.

Con respecto a México, de acuerdo a las exploraciones y datos de herbarios, para *S. lycopersicum* en 2012 la Red de Jitomate en México tenía un registro de 491 colectas

(Lobato et al., 2012). A partir de esta investigación se recabaron el triple de colectas registradas, a través de la búsqueda y localización de bases de datos nacionales e internacionales como la Red Mundial de Información sobre sobre Biodiversidad de CONABIO (http://www.conabio.gob.mx/remib/) y repositorios dedicados a esta especie como Tomato Genetics Resource Center (https://tgrc.ucdavis.edu/), Solanaceae Source (https://solanaceaesource) y repositorios de especies en general como the Global Biodiversity Information Facility (https://www.gbif.org).

En el caso de los parientes silvestres de tomate, su información se encontraba disponible en algunas publicaciones científicas como las de Marshall et al. (2001), Peralta et al. (2001; 2008) y Grandillo et al. (2011). Además, la colaboración con el Ministerio de Agricultura de Perú, permitió acceder a la información de cerca de 900 datos de pasaporte adicionales. Los artículos ya publicados de los capítulos 3 y 4, constituyen una fuente de datos actualizada y sistematizada sobre estas especies.

Con respecto a la metodología, se emplearon técnicas especializadas, que combinadas, permitieron la adecuada interpretación de datos y generar nueva información que servirá de base para futuras investigaciones. El uso de métodos estadísticos multivariados fue de gran utilidad para realizar el manejo de bases de datos de gran tamaño y, en todos los casos, generaron resultados satisfactorios que permitieron la una interpretación sencilla con asociaciones coherentes con la realidad observada. De ahí que los descriptores ecológicos identificados para las 17 especies atendidas constituyen una fuente confiable de información no reportada con anterioridad.

Al comparar *S. lycopersicum* en México contra las especies silvestres y emparentadas distribuidas en Latinoamérica, es posible observar que las variables de mayor contribución para explicar la distribución y diversidad de las colectas de especies analizadas son la temperatura media anual, altitud, precipitación anual y evapotranspiración anual; aunque con importancia relativa diferente de acuerdo con las especies en particular. Estas mismas variables han sido identificadas como

determinantes en la distribución de maíz y teocintle (Sánchez-González et al., 2018; Ramírez-Ojeda et al., 2021).

En el caso de las especies silvestres de *S. lycopersicum*, también se analizaron variables edáficas y su correlación con variables ambientales. En este caso, se identificaron las cuatro variables mencionadas previamente junto con la precipitación del mes más seco y la isotermalidad como las de mayor influencia en la distribución de especies.Con respecto a las variables de suelo, el pH, la densidad aparente, el porcentaje de bases, el contenido de arena y la concentración de carbonato de calcio fueron las características que tuvieron mayor influencia en la distribución de especies. Se podría suponer que estas variables pueden ser similares para aquellos los suelos donde se localizan las colectas de *S. lycopersicum* en México. Situación que deberá ser corroborada.

Los tipos de climas B o áridos, son los predominantes en donde se establecen las especies silvestres y emparentadas a *S. lycopersicum* en Latinoamérica. En contraste, *S. lycopersicum* en México tiende a distribuirse con mayor frecuencia en climas tipo C o templados.

Aunque en este trabajo no se abordó el impacto del cambio climático, es necesario evaluar las condiciones de los escenarios climáticos futuros para determinar sitios con material susceptible a pérdida debido a estas condiciones.

Finalmente, los análisis hotspot, tanto para el grupo de especies silvestres en Latinoamérica como para *S. lycopersicum* en México, mostraron zonas de alta y baja diversidad que indican zonas susceptibles a conservación.

6. CONCLUSIONES GENERALES

A través de estudios ecogeográficos fue posible obtener información edafoclimática que permitió la caracterización confiable de los ambientes correspondientes a los sitios de colecta de las especies silvestres que conforman el grupo taxonómico de los tomates en México y Latinoamérica.

Se reconstruyeron los ambientes en los cuales habitan las especies silvestres y filogenéticamente cercanas a *Solanum lycopersicum* y se asoció esta información con características edafoclimáticas con lo que, a su vez, se determinaron los descriptores ecológicos de cada una de ellas.

La metodología empleada basada en sistemas de información geográfica junto con análisis multivariados, demostraron ser una herramienta útil para determinar las variables ambientales y su asociación con los patrones de distribución y diversidad de las especies de tomate analizados en forma confiable.

La metodología demostró ser útil para identificar colectas con uso potencial para programas de mejoramiento genético, al ser asociadas con factores adversos en el ambiente.

Se identificaron zonas de alta y baja diversidad con lo cual se podrán desarrollar estrategias de uso y conservación de los recursos genéticos de *S. lycopersicum* y especies silvestres y emparentadas.

Se detectó la necesidad de realizar el análisis de los factores edáficos en las colectas de *S. lycopersicum* en México. Así mismo se requiere identificar las zonas de distribución potencial de cada especie silvestre y emparentada *a S. lycopersicum* en Latinoamérica.

Con las bases de datos obtenidas, la metodología diseñada y la información generada, será posible evaluar la tendencia de los escenarios de cambio climático y sus impactos en la distribución y ecología de las especies que forman el grupo de tomates.

Esta investigación constituye un modelo aplicable y replicable en cualquier otra especie vegetal.

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