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MANEJO DE FERMENTOS EN MÉXICO: UNA PERSPECTIVA ECOLÓGICA Y CULTURAL

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PRESENTA:

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Presente

Me permito informar a usted que, en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **07 de marzo de 2022,** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS,** del estudiante **OJEDA LINARES CÉSAR IVÁN,** con número de cuenta **304218743,** con la tesis titulada "**MANEJO DE FERMENTOS EN MÉXICO: UNA PERSPECTIVA ECOLÓGICA Y CULTURAL",** realizada bajo la dirección del **DR. ALEJANDRO CASAS FERNÁNDEZ**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

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"POR MI RAZA HABLARÁ EL ESPÍRITU"
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Bien se puede filosofar y aderezar la cena.
Y yo suelo decir viendo estas cosas:
sí Aristóteles hubiera guisado, mucho más hubiera escrito.

Sor Juana Inés de la Cruz

A continuación, una tesis que se fermentó desde antes y durante la pandemia del COVID-19. Contiene notas aromáticas con un sabor refrescante. Al mismo tiempo, contiene una burbujeante sensación de ser un ente inconcluso.

"*Kilgore Trout escribió una vez un cuento lo que sería un diálogo entre dos levaduras. Discutían los posibles propósitos de la vida mientras comían azúcar y se asfixiaban con sus propios excrementos. Debido a su inteligencia limitada, nunca llegaron a adivinar que estaban haciendo Champagne* ".

Kurt Vonnegut, Desayuno de Campeones

Índice general

Resumen

Históricamente los seres humanos hemos desarrollado procesos tradicionales de manejo de microorganismos como la fermentación, o procesos como el ahumado, la deshidratación o el uso de sal para conservar o mejorar el valor nutricional de los alimentos. Las prácticas de manejo de microorganismos probablemente ocurrieron antes de la transición a la producción de alimentos mediante la horticultura o la agricultura. Los alimentos fermentados son clave en la cultura alimentaria alrededor del mundo, a pesar de que comúnmente se les relega en los estudios de la dieta; se estima que estos alimentos representan hasta un tercio de aporte energético. Los productos fermentados permiten vislumbrar la complejidad socioambiental de distintos territorios donde seelaboran. Marcan una íntima relación del ser humano con su ambiente, su territorio; los saberes para su producción permiten divisar un complejo ensamble entre humanos-sustrato-microrganismos. Lamentablemente las presiones sociales, económicas y culturales sobre los productos fermentados tradicionales han promovido su marginación e incluso algunos han llegado a desaparecer de los panoramas alimentarios locales. En México, se estima que existen alrededor de 200 productos fermentados producidos a partir de una amplia variedad de plantas y animales. Entre los productos más diversos y conocidos a nivel nacional son las bebidas fermentadas, éstas se producen a partir de distintas estructuras vegetales como hojas, tallos, savias, raíces, cortezas, frutos o semillas y representan elementos clave de la dieta y de la cultura mexicana. Sin embargo, pocas de estas bebidas han sido estudiadas de manera detallada, generalmente bebidas de importancia económica son abordadas debido a que son consideradas por su importancia económica o en algunos casos son consideradas como fuentes potenciales de microorganismos pre o probióticos con aportes benéficos a la salud. De hecho, en años recientes el estudio del pulque se ha dirigido la investigación para abordar las posibles ventajas de estos microorganismos para la producción de etanol, ácido láctico, ácido acético, vitaminas, y aminoácidos por mencionar algunos metabolitos. Por otro lado, algunas bebidas tradicionales se han mantenido aún más marginalizadas e incluso no se han realizado estudios para caracterizar los procesos de producción o los cambios en las comunidades microbianas que están involucradas en la fermentación y que son manejadas por los productores durante la fermentación. Esta tendencia de investigación ha promovido que gran parte de las bebidas fermentadas hayan sido escasamente caracterizadas en los procesos involucrados en su producción y las comunidades de microorganismos que intervienen en la fermentación. En este sentido, es probable que la pérdida de estos productos represente también la pérdida del conocimiento ecológico tradicional para elaborarlos, la degradación de los sistemas alimentarios locales y la disminución de la diversidad

asociada, como plantas, animales y desde luego los microrganismos.

Por esta razón, el presente proyecto tiene como objetivos; (1) presentar un panorama de la diversidad de microorganismos y de los sustratos empleados por los diferentes grupos culturales del país, y de su distribución espacial como Bebidas Fermentadas Tradicionales Mexicanas; (2) abordar el caso particular del manejo de microorganismos en una bebida fermentada tradicional elaborada a partir de frutos de cactáceas conocida como colonche; caracterizar el proceso de fermentación, los aspectos socio-económicos de los productores y los atributos sensoriales que prefieren en su bebida; (3) Contrastar las implicaciones que tiene el manejo de las fermentaciones sobre la comunidad de microorganismos en la producción de colonche. Para abordar tales objetivos, se realizó una revisión bibliográfica registrando las bebidas fermentadas tradicionales, las plantas, las comunidades microbianas, grupos culturales asociados a su producción y su distribución. Se realizó un trabajo etnobiológico en la región del Altiplano central y el Valle de Tehuacán en donde se caracterizó la producción del colonche, se documentaron las especies vegetales empleadas, se realizó una detallada caracterización de las prácticas de fermentación y se contrastaron los aspectos sensoriales buscados por los productores tanto en fermentaciones espontáneas como en las inoculadas. Finalmente, mediante el uso de técnicas de secuenciación de nueva generación, por medio de secuencias especificas o códigos de barras, se caracterizó la comunidad de bacterias y hongos asociados a estos espacios de fermentación y se contrastaron las diferencias entre distintas prácticas de manejo, incluyendo aquellas que involucran fermentaciones espontáneas e inoculadas.

Se documentó que para la producción de 15 bebidas fermentadas tradicionales se utilizan 143 especies de plantas, 52 grupos culturales están involucrados en la producción y se identificaron 102 géneros de microorganismos presentes en las distintas bebidas fermentadas. Los grupos de plantas más importantes para producir estas bebidas son el maíz (*Zea mays*), el maguey (*Agave* spp.) y los frutos de cactáceas, principalmente del género *Opuntia*. No obstante, hay un contraste entre el estudio de bebidas elaboradas a partir de plantas del género *Agave*, debido asu interés económico y biotecnológico, en comparación con el resto de las bebidas fermentadas tradicionales. Estas mismas características se reflejan en los estudios que abordan la caracterización de la microbiota, en donde el número de bebidas y estudios se encuentra mayoritariamente enfocados a este grupo de bebidas de agave, principalmente mescal y pulque.

Para la elaboración del colonche identificamos dos grandes regiones productoras, el Valle de Tehuacán-

Cuicatlán y el Altiplano Central de México. En la primera región se realiza a partir de distintos frutos de cactáceas columnares y en la segunda mayoritariamente de frutos de *Opuntia*, siendo *Opuntia streptacantha* la especie preferida por los productores de la región del Altiplano. Las prácticas de fermentación empleadas para la producción del colonche en ambas regiones es la fermentación inducida con inóculos, y en la región del Altiplano se realizan fermentaciones naturales o espontáneas. Igualmente, observamos las diferencias en los atributos sensoriales bajo las distintas prácticas de manejo y fermentación en la región del Altiplano, en donde encontramos una preferencia por bebidas más dulces, un color morado más intenso y con mayor contenido alcohólico en fermentaciones espontáneas, mientras que las fermentaciones con inóculos favorecen atributos como la acidez, la textura y el color. Finalmente, a través del presente estudio identificamos la relevancia cultural y socio- económica de esta bebida en las distintas regiones, observando una creciente revitalización de su producción.

La evaluación de la comunidad de microorganismos del colonche bajo distintas prácticas de manejo permitieron identificar diferencias significativas en la composición, diversidad y riqueza en la comunidad de microorganismos bajo fermentaciones espontáneas y aquellas con el uso de inóculos. Particularmente se observó una mayor riqueza de bacterias en las fermentaciones espontáneas en comparación con las fermentaciones inoculadas. No obstante, en ambos tipos de fermentaciones se identificaron bacterias ácido lácticas como el grupo más abundante. En el caso de hongos, identificamos un menor número de especies comparado con el identificado en bacterias, siendo las fermentaciones inoculadas las que desplegaron una mayor riqueza de levaduras en el producto final. Además, el muestreo realizado también permitió caracterizar la comunidad asociada a las ollas en las que se realiza la fermentación y a los inóculos utilizados en la fermentación. Estos dos últimos espacios permitieron observar que la olla tiene una mayor diversidad de bacterias y hongos, que para algunas especies se van perdiendo durante el proceso de sucesión de la comunidad involucrada en la fermentación y en otros casos, pueden ser reservorios de especies de hongos para las siguientes etapas de la fermentación. En el caso del inóculo, los resultados mostraron que tiene una baja riqueza y una dominancia en el caso de levaduras del género *Saccharomyces*, sugiriendo así que existen procesos de selección que favorecen consorcios de microorganismos para alcanzar fermentaciones óptimas en un menor tiempo. En este sentido, se observó que las prácticas de manejo de la fermentación que realiza la gente tienen implicaciones para remodelar estos micro ambientes.

En conclusión, la investigación muestra que los productos fermentados son importantes reservorios

de diversidad biocultural, representan un valioso conocimiento ecológico tradicional, son clave en la seguridad alimentaria local y dan identidad local a la comunidad. El estudio de los procesos de fermentación bajo una perspectiva etnobiológica provee perspectivas sobre los procesos de selección y domesticación de consorcios de microorganismos, así como de linajes de microrganismos específicos. A pesar de que la gastronomía mexicana es considerada como patrimonio inmaterial de la humanidad, los elementos fermentados son escasamente considerados. Estos, deben ser promovidos y generar marcos legislativos para su conservación.

Abstract: Historically, human beings have developed traditional processes for handling microorganisms such as fermentation to preserve or improve the nutritional value of food. Fermented foods are key in food culture around the world, even though they are often relegated to dietary studies; It is estimated that these foods represent up to a third of energy intake. Fermented products allow us to glimpse the socio-environmental complexity of the different territories where they are made. They mark an intimate relationship between the human being and his environment, his territory; the knowledge for its production allows us to see a complex ensemble between humans-substrate-microorganisms. In fact, microorganism management practices likely occurred before the transition to food production through horticulture or agriculture. The present thesis developed three main objectives; (1) present an overview of the diversity of Traditional Mexican Fermented Beverages, the microorganisms involved, the plant substrates used by the different cultural groups in the country, and their spatial distribution. Also, to address the particular case of microorganisms managing in a traditional fermented beverage made from cacti fruits known as colonche; characterize the fermentation process, the socio-economic aspects of the producers and the sensory attributes that they prefer in their drink. Finally, to contrast the implications that the management of fermentations has on the community of microorganisms in the production of colonche. The results are published in the following sections and in open access journals . In conclusion, fermented products are important reservoirs of biocultural diversity, represent valuable traditional ecological knowledge, are key to local food security and give local identity to the community. The study of fermentation processes from an ethnobiological perspective provides perspectives on the processes of selection and domestication of consortia of microorganisms, as well as lineages of specific microorganisms. Despite the fact that Mexican gastronomy is considered as intangible heritage of humanity, fermented elements are scarcely considered. These must be promoted and generate legislative frameworks for their conservation.

Introducción general

El sabor, la consistencia y la esencia de esta tesis: conceptos clave para leer este proyecto

La agrobiodiversidad: el platillo principal de cualquier comida

A lo largo de la historia los seres humanos hemos transformado el mundo entero, sus componentes, procesos y sus dinámicas. Hacemos uso de especies, paisajes, comunidades y en general, de un gran número de recursos naturales que forman parte de ecosistemas naturales y al complejo entramado de relaciones ecológicas y sociales en torno a los recursos necesarios para el sostenimiento de la vida civilizada, conocidos como sistemas socioecológicos (Ostrom, 2009; Barton, 2009). Estos recursos no se encuentras aislados o estáticos, sino que involucran una alta integración dinámica de distintos procesos ecológicos, evolutivos, sociales, culturales, entre otras propiedades emergentes características de estos sistemas complejos y heterogéneos (Funtowics y Ravetz, 1993; García, 2006; Casas *et al*., 2014, 2016, Casas y Vallejo, 2017). Estos recursos naturales están inmersos en distintas unidades paisajísticas e involucran una amplia variedad de componentes y procesos que permiten realizar diversas actividades humanas primarias que proveen alimentos y materias primas para múltiples destinos y funciones (Casas y Parra, 2016; Casas *et al*., 2016, 2017).

Los recursos genéticos son también considerados como componentes principales de la agrobiodiversidad pues poseen genes con valor actual o potencial. La agrobiodiversidad comprende tanto la diversidad silvestre y domesticada de plantas, animales, hongos y microorganismos asociada directa e indirectamente a los sistemas de producción de alimentos y materias primas, incluyendo los sistemas agrícolas, pecuarios y silvícolas, todos los cuales se encuentran en interacción en los procesos de producción rural e industrial, influyéndose mutuamente (FAO, 1999, 2016; Crowley *etal*., 2007; Moreno-Calles *et al*., 2013; Casas *et al*., 2016; Casas y Vallejo 2017). Asimismo, esta agrobiodiversidad puede ser estudiada, caracterizada y cuantificada a través de su riqueza y diversidad de especies domesticadas y silvestres, las cuales brindan importantes servicios ecosistémicos (Casas y Parra, 2007; Casas *et al*., 2014).

Los recursos genéticos son diversidad genética aprovechable para múltiples propósitos, y un reto principal es asegurar su mantenimiento a diferentes escalas de organización y dichas estrategias pueden monitorearse con base en indicadores específicos. Una de las formas más utilizadas para monitorearlos es a través de indicadores planteados desde la genética de poblaciones, los cuales permiten evaluar la magnitud de la diversidad y estructura genética, así como la intensidad de flujo génico. Los ecólogos teóricos, siguiendo el modelo de Whittaker (1960), a menudo subdividenjerárquicamente la diversidad de especies en tres componentes, el primero haciendo referencia a la diversidad dentro de la muestra (α), el segundo, entre muestras (β) y la diversidad global o del paisaje (γ), este último componente siendo aditivo de los primeros dos ($\gamma = \alpha + \beta$, Crist *et al.* 2003). Las principales unidades de medida son la riqueza (recuento de especies simples) y la heterogeneidad (abundancia relativa de cada especie en una comunidad). Estos indicadores, permiten visualizar la integridad del sistema, pero además permiten vislumbrar procesos que ocurren en los componentes y procesos dentro de estos sistemas complejos (Funtowics y Ravetz, 1993; García 2006; Morin, 1995).

Todos estos recursos ya sean de origen vegetal, animal, fúngico o microbiano, son parte fundamental de la agrobiodiversidad, muchos de estos son intensamente utilizados por distintas localidades alrededor del mundo, así como recursos genéticos para atender necesidades presentes y futuras de nuestra sociedad. No obstante, muchos de estos recursos han sido escasamente estudiados y menos aún considerados en los programas de protección y conservación de recursos genéticos y esta tesis hace hincapié en el caso de los microorganismos asociados a la elaboración de fermentos. A grandes rasgos, en la presente tesis consideramos al patrimonio biocultural como la reunificación de cultura y naturaleza, bajo esta concepción puede verse a la biodiversidad en su espacio utilitario y en sus distintas formas de representación, así mismo, bajo este concepto se considera que la transmisión para usar y manejar la diversidad biológica y el territorio ocurre de generación en generación dentro de los pueblos originarios, campesinos y campesinos indígenas. (Toledo y Barrera-Bassols, 2009; Boege, 2010; Machuca, 2021). En este sentido, cualquier política pública dirigida a conservar los recursos genéticos que conforman la agrobiodiversidad debe basarse en un diagnóstico de la diversidad intra e interespecífica de especies domesticadas, así como del importante y amplio grupode especies manejadas, entre las cuales se encuentran parientes de las especies plenamente domesticadas (Heywood *et al.*, 2007) y, en general, recursos de alto potencial para afrontar necesidades futuras, como es el caso de los microorganismos (Casas *et al*., 2016, 2017, 2017).

¿A que nos referimos cuando hablamos de manejo?

El manejo de recursos es una actividad eminentemente realizada por grupos humanos, pues involucra acciones deliberadas para transformar o mantener sistemas ecológicos o socioecológicos, elementos o funciones de esos sistemas, e involucra un elevado grado de conciencia e intencionalidad en tales transformaciones (Casas *et al*., 2014; 2015; Casas y Parra, 2016). Por lo tanto, el manejo es un actuar deliberado sobre los sistemas naturales o artificiales (ecosistemas o socioecosistemas,respectivamente), sus componentes (recursos o servicios ecosistémicos de provisión) y/o los procesos o funciones que ocurren en estos (reconocidos también como servicios ecosistémicos de regulación y soporte) (Casas *et al*. 1997, 2014, 2015). Su propósito es usarlos, transformarlos, mantenerlos o recuperarlos de acuerdo con sus necesidades o intereses de las sociedades de las que los humanos forman parte (Lindig y Casas, 2013).

El manejo incluye diversas formas de interacción y prácticas como (1) el aprovechamiento, el cual involucra técnicas y estrategias dirigidas a obtener y utilizar recursos, sistemas o procesos que ocurren en estos; (2) la conservación, que incluye acciones dirigidas a mantener los recursos, sistemas y/o procesos; (3) la restauración, que implica prácticas para recuperar componentes, funciones o procesos del sistema, incluso a los sistemas en su conjunto y (4) el ordenamiento, que implica definir estrategias para planificar las acciones de manejo y el destino de las distintas unidades que componen un ecosistema, un paisaje o un territorio (Casas y Parra, 2016) y este puede verse en un gradiente de escalas, es decir desde micro a macro escalas.

El estudio de las tipologías que ha adoptado el manejo en la historia humana permite reconocer que dentro del contexto actual los seres humanos nos encontramos bajo una gran crisis ambiental a escala global que presenta múltiples panoramas poco alentadores como el calentamiento global, la degradación de distintos ecosistemas, la pérdida de biodiversidad, entre otros y por esos motivos decidimos hacer distintas prácticas para mantener o conservar diversos recursos (Tilman, 2000;Landsea, 2005; Haddad *et al*., 2009; McNutt, 2015; Biao *et al*., 2022). Además, estos escenarios manifiestan la dimensión social de la problemática global, como el aumento en la pobreza, la inequidad, la pérdida de culturas y diversidad cultural, un incremento en los conflictos, las confrontaciones socioculturales entre otros factores y un incremento en la inseguridad y pérdida de soberanía alimentaria (Casas *et al*., 2015). En este sentido el manejo sustentable busca satisfacer las necesidades de las sociedades presentes sin comprometer las posibilidades de las generaciones futuras.Para hacerlo posible, los seres humanos buscan diseñar estrategias para detonar procesos usando una amplia gama de tecnologías, toma diversas estrategias políticas-económicas para el mantenimiento de la base material que sostiene la vida de las sociedades y los procesos que permiten la vida en elplaneta y procurar el bienestar humano.

Conocimientos Ecológicos tradicionales

El Conocimiento Ecológico Tradicional es relevante en los estudios biológicos que involucran una mirada amplia, con una larga historia, para abordar el estudio de la complejidad identificada entre la relación humano-naturaleza. En general, distintos grupos de individuos en diferentes áreas del planeta ven y se conectan con la naturaleza de diversas formas y tienen distintas costumbres e información ecológica ligada a los ambientes en los que viven (Nepal, 2021). Sus percepciones e información están, en cierta medida, moldeadas por sus visiones del mundo, sus valores, sus creencias religiosas y su ética ambiental en un sentido amplio. El Conocimiento Ecológico Tradicional (TEK por sus siglas en inglés, Traditional Ecological Knowledge, TEK en adelante) se puede definir como aquellos sistemas de conocimiento que se transmiten de una generación a otra durante cientos y miles de años a través del contacto directo con su ambiente (Berkes, 2012). Este es generalmente, dinámico, acumulativo, de amplía experiencia y con la capacidad de ajustarse al cambio.

En la actualidad se reconoce que los sistemas de TEK asumen un papel importante para alcanzar y apoyar las metas de la sostenibilidad (Lyver *et al.*, 2019; Brondizio *et al.*, 2021). Por ejemplo, gran parte de la biodiversidad silvestre y domesticada del mundo se encuentra en tierras y aguas habitualmente gestionadas por comunidades locales y pueblos indígenas. (Garnett *et al.*, 2018; Ellis et al., 2021; Molnár y Babai, 2021). Estas regiones son baluartes con capacidades ecológicas vitales que se suman a la prosperidad humana y no humana, incluida la mitigación del cambio climático y la soberanía alimentaria (Fa *et al.*, 2020). De hecho, se ha registrado que en las comunidades locales y los pueblos indígenas que mantienen estas características de los TEK, la pérdida de la biodiversidad disminuye a menor velocidad en comparación con los sistemas biológicos fuera de ellos, los cuales generalmente están sujetos a una alta presión generada por las actividades relacionadas al desarrollo y la extracción de recursos a velocidades industriales (Díaz *et al.*, 2019). A grandes rasgos, el conocimiento ecológico tradicional local se encuentra amenazado y en peligro de perderse como consecuencia inmediata de la intensificación de los poderes de la globalización, el expansionismo, un constante maltrato por parte de las instituciones gubernamentales y una amplia gama de intereses políticos que buscan sobreponerse a las comunidades locales y los pueblos indígenas (Tang y Gavin, 2016; Cámara-Leret *et al.*, 2019; Lyver *et al.*, 2019).

Aunque el conjunto de conocimientos ecológicos tradicionales son únicos y, en cierto modo, se encuentran equipados para adaptarse a situaciones políticas y socioambientales cambiantes (Quinlan y

Quinlan, 2007), se están perdiendo a un ritmo inquietante (Reyes-García *et al*., 2013; Gaup Eira *et al*., 2018). Tales pérdidas cambian los cimientos del sustento y la cultura de las personas y dan como resultado la erosión cultural, la pobreza y el despojo (Reo *et al*., 2019; Armstrong y Brown 2019; Ford *et al*., 2020). Posteriormente, las comunidades locales y los pueblos indígenas experimentan cambios sociales y naturales desequilibrados (Savo *et al*., 2016; Dunn, 2017) que generan nuevos panoramas de incertidumbre y particularmente afectan la posibilidad de satisfacer necesidades básicas como la alimentación. Las amenazas al conocimiento ecológico tradicional son motivo de preocupación, pues las comunidades indígenas enfrentan desafíos más severos a través de las políticas, la legislación del gobierno y la presión de las políticas de desarrollo económico. No obstante, se han identificado casos en diversas localidades que generan distintas estrategias para mantener estos conocimientos y una de las formas más comunes para transmitirlos es a través de los recursos alimentarios, es decir, el cómo hacer uso de recursos domesticados y no domesticados y como integrarlos a la dieta a través de distintos platillos (Setalaphruk y Price, 2007).

Con las manos en la masa: la relación seres humanos-microorganismos

Es probable que para muchos seres humanos los microorganismos sean vistos como enemigos causantes de patologías tanto en plantas como en animales, incluidos los humanos. Son vistos preponderantemente como los responsables de llevar al mundo entero a la pandemia y confinamiento por dos años a causa del SARS-COVID-19. No obstante, los seres humanos hemos utilizado a los microorganismos para un amplio número de actividades; de hecho, nuestra relación con este numerosogrupo es muy estrecha y sin duda muy importante en distintos aspectos de nuestra cotidianidad y aún en funciones que desconocemos (Taylor, 2001; Lindner y Bernini, 2022).

Quizá por su tardía detección y la baja certeza de caracterización, estos grupos han sido en menor grado estudiados en comparación con las plantas y animales. Para la identificación de estos grupos de organismos tuvieron que ocurrir diversos desarrollos tecnológicos como el perfeccionamiento de los microscopios por parte de Anton van Leeuwenhoek en 1676, así como otros trabajos pioneros de Needham, Spallanzani, Pasteur y Bassi de Lodi en los siglos XVIII y XIX, quienes hasta ese momento identificaron a los microorganismos como agentes implicados en la producción y el deterioro de alimentos. Este numeroso grupo conocido como microorganismos está compuesto por bacterias, virus, levaduras, protistas, amebas, planarias, Archeas, incluso algunas algas y hongos, de los cuales cada uno de estos grupos tienen sus múltiples clasificaciones adicionales (Tamang, 2015).

Los microorganismos son ubicuos, es decir están presentes en casi todos los lugares del mundo. Constituyen un grupo heterogéneo de seres vivos cuya única característica común es su reducido tamaño, son los más abundantes en el planeta y en realidad son aliados potenciales que permiten garantizar nuestra continuidad en el mundo (Head *et al*., 1998). Juegan un papel clave en el ambiente ya que son los principales responsables de la descomposición de moléculas complejas, la producción de oxígeno, el reciclaje de nutrientes, relaciones simbióticas con plantas y animales. Esta última es de gran importancia ya que la relación de microorganismos con plantas, tales como las que ocurren con bacterias fijadoras de nitrógeno o micorrizas en el rizoma de diversas plantas permiten desplegar un mejor crecimiento en comparación de plantas que no las presentan (Mauchline y Malone,2017; Sasse *et al*., 2018; Compant *et al*., 2019). Incluso, en los últimos años se ha identificado la importancia del microbioma de los humanos para mantener un estado de salud óptimo (NIH, Human Microbiome Portfolio Analysis team, 2019). Así mismo, son útiles para un amplio número de promesas biotecnológicas emergentes para mejorar distintos aspectos de nuestra vida como son la restauración ecológica, el combate de patologías crónicas, la producción de medicamentos, alimentos, entre otros (Higa, 1991; Hui y Khachatourians, 1996; Paxson y Helmreich 2014, 2017).

Hoy en día se utiliza la palabra biotecnología como si representara un concepto moderno que generalmente va asociado a nuevas aplicaciones y productos de relevancia económica o especialmente a ingeniería genética o a la tecnología de ADN recombinante. No obstante, el diccionario Oxford English Dictionary ofrece una definición más amplia que en términos simples permite usarlo como una amplia definición para la presente tesis, definiéndola como "*la rama de la tecnología que se ocupa de las formas modernas de producción industrial que utilizan organismos vivos, especialmente microorganismos, y sus procesos biológicos*". Esta definición permite remontarse históricamentemucho más atrás de que se caracterizara al ADN como "*el secreto de la vida*" por Watson y Crick y permite ver que la biotecnología ya formaba parte de un conjunto de saberes antiguos previos a los desarrollos tecnológicos actuales y mucho más importante hace referencia a que la fermentación representaba un proceso utilitario para mejorar y conservar una amplia diversidad de recursos. Entonces, bajo esta definición el uso de la fermentación es una de las primeras formas de hacer uso de la biotecnología a nivel mundial.

Sociedades de todo el mundo descubrieron de forma independiente el valor de fermentar los alimentos como un método económico de conservación más antiguo, mejorando así la calidad nutricional y las características sensoriales de los alimentos (Farhad *et al*., 2004; Yurdakul *et al*., 2017).

De hecho, el registro de la bebida fermentada más antigua proviene de vasijas de cobre dondese fermentaba arroz, miel y otros frutos desde el 9000 A.P. en China (McGovern *et al*., 2004). Asimismo, un análisis proteómico reciente ha demostrado que la leche similar al kéfir se fermentó hace unos 3500 años en Asia (Yang *et al*., 2014). Igualmente, la producción de pan y vino son productos fermentados que históricamente han cambiado a la sociedad y se considera que su producción empezó en el creciente fértil donde la domesticación de plantas como el trigo y la vid se llevó a cabo (Charmet, 2011; Grassi y Arroyo-Garcia, 2020). Así pues, podemos decir que nuestros antepasados a su manera hacían uso de organismos vivos para producir alimentos y fueron losprimeros biotecnólogos y en muchos casos estos procesos siguen vigentes y además, resultan relevantes en los sistemas alimentarios globales.

Los fermentos: elementos en transformación, microbiomas dinámicos

La fermentación es un proceso bioquímico por el cual sustancias orgánicas como el azúcar son transformadas o metabolizadas en otros compuestos reducidos como: etanol, dióxido de carbono, alcoholes, ésteres, entre otros. Además, durante este proceso de oxidación parcial, se libera una ligera cantidad de energía que queda disponible (James *et al*., 2005; Kurtzman *et al*., 2011). Esta acción es realizada principalmente por microorganismos como bacterias, levaduras y mohos, los cuales tienen un papel clave en la modificación física, nutricional y sensorial de la materia prima. Particularmente, sus interacciones son clave para obtener productos seguros y con atributos sensoriales únicos.

En la actualidad se han descrito distintos tipos de fermentación dependiendo del grupo microbiano que predomina en estos ambientes. Dentro del tipo de fermentaciones más conocidas es la fermentación alcohólica o etílica, en la cual alguna fuente de azúcar es catabolizada en condiciones anaeróbicas generando como resultado etanol, dióxido de carbono y moléculas de adenosín trifosfato (ATP). La fermentación alcohólica es común en diversas bebidas a nivel industrial o local, por ejemplo las cervezas, los vinos, los destilados, entre otros. Igualmente, una de las fermentaciones máscomunes es la fermentación láctica (Ahmad *et al*., 2020), en la cual ocurre la transformación de ácido pirúvico procedente de la glucólisis en ácido láctico y regenerar NAD^+ para proseguir con la glucólisis. Este tipo de fermentación es común en distintos productos fermentados de origen animal, por ejemplo, el yogurt, los quesos, pero también es común en productos vegetales como el PaoCai de China o el sourkrout de Alemania (ambos casos col fermentada), o en la elaboración de pan a partir demasas madres (Arora *et al*., 2021).

Así mismo, la fermentación acética es comúnmente realizada por bacterias aeróbicas delgénero *Acetobacter*, este grupo transforma el alcohol etílico en ácido acético (Sengun y Karabiyikli, 2011). Este tipo de fermentación puede verse en el vinagre que puede venir de distintos sustratos como vinos de uvas u otras frutas en donde la presencia de oxígeno degrada las cualidades del producto y prolifera este grupo bacteriano (Gomes *et al*., 2018). Igualmente, pueden ocurrir fermentaciones malo-lácticas, en donde se transforma el ácido málico en láctico y es común enbebidas como el vino o las sidras producidas por manzanas (De Roos y De Vuyst, 2018). También, la fermentación butírica es aquella en donde se produce ácido butírico a partir de la glucosa en un ambiente anaeróbico y tiene como característica principal desprender olores usualmente reconocidos como desagradables. A pesar de los olores desagradables, a este tipo de fermentación se le pueden atribuir también sabores dulces los cuales son utilizados como saborizantes en algunos alimentos y bebidas como en la producción de quesos. Además, en años recientes esta fermentación ha tenido aplicaciones en la fabricación de plásticos los cuales han sido utilizados para la producción de fibrastextiles (Zhang *et al.*, 2009).

Dentro de las fermentaciones ocurren diversas interacciones entre diferentes gruposmicrobianos y también con las condiciones ambientales, tanto en el ambiente interior como con diversos factores del exterior. Un ejemplo que permite visualizar esta complejidad de interacciones en estos micro-ambientes es la producción de quesos y particularmente casos como el queso roquefort, o quesos azules en donde se ha evaluado que existen diferentes microorganismos en la corteza exterior del queso donde existe una interacción constante con el ambiente, mientras que en el interior interactúan otros microrganismos los cuales se encuentran semi-aislados del exterior y se mantienen las interacciones en el interior (De Filippis *et al*., 2014; Ercolini, 2020; Johnson *et al*., 2021).Asimismo, ocurre que para la elaboración de estos productos ocurren cambios en las comunidades de microorganismos estos cambios son tan variables que es poco probable que las interacciones se separen por grupos discretos, ya que puede producirse más de un tipo de interacción simultáneamente (Verachtert, 1990; Viljoen *et al*., 1993; Leroi y Pidoux 1993; Barntett, 2003).

Las interacciones microbianas generalmente son evaluadas en función del efecto que tienen sobre el tamaño de la población, pero independientemente de si las interacciones son positivas,neutrales o negativas, los tipos de interacción presentes en comunidades de microorganismos también se clasifican en función de interacciones directas o indirectas (Bull y Slater 1982, Zelezniak *et al*., 2015). Estas interacciones son importantes para mantener la coexistencia estable de las comunidades (Albergaria y Arneborg 2016). Las interacciones indirectas se refieren a la competencia, el comensalismo, el mutualismo, el amensalismo o antagonismo y el neutralismo y muchas de estas se deben a la presencia de metabolitos extracelulares (Linton y Drozd. 1982). Ejemplos como estos son comunes cuando las bacterias ácido lácticas producen un ambiente más ácido y no permiten que otras especies de bacterias puedan mantenerse en estos ambientes (Querol y Fleet, 2006). Las interacciones directas incluyen la depredación y el parasitismo, la simbiosis, el mismo contacto físico entre microorganismos y la detección de quórum (Querol y Fleet 2006; Viljoen, 2006). Estas interacciones contribuyen a la regulación de las poblaciones (Querol y Fleet 2006; Viljoen, 2006; Albergaria y Arneborg 2016; Ponomarova *et al*., 2017) y en años recientes los mecanismos que subyacen en estas interacciones han sido objeto de numerosos estudios en las últimas décadas y actualmente están empezando a demostrarse con mayor claridad (Canon *et al*., 2020).

Las comunidades de microorganismos asociadas a las fermentaciones son un buen sistema para estudiar las sucesiones ecológicas en donde a lo largo de la fermentación las comunidades tienden a interactuar, existiendo recambios de especies y eventualmente llegan a un estado homeostático (Viljoen, 2006; Ponomarova *et al*., 2017). En estas fermentaciones se asume que la comunidadmicrobiana se encuentra estable y la mayoría de los nichos ecológicos están llenos. Por consiguiente, difícilmente microorganismos externos se establecen, ya sea introducidos accidental o intencionalmente (Fleet, 2006; Padonou *et al*., 2010; Ponomarova *et al*., 2017). Sin embargo, esto no siempre sucede así, pues depende de la robustez que tienen las comunidades provenientes de inóculos o, por el contrario, puede ocurrir el establecimiento de microorganismos que dañen el producto, esto dependerá de las características biológicas intrínsecas de estas especies (Padonou *et al*., 2010). Una razón de la estabilidad en estas fermentaciones es la continua diversificación y la heterogeneidad resultante de los miembros de la comunidad bajo fluctuaciones ambientales (Querol y Fleet 2006; Padonou *et al*., 2010; Ponomarova *et al*., 2017).

Generalidades de tipos de fermentación: inoculaciones, espontáneas y cultivos puros

Como seres humanos tomamos decisiones para transformar diversos sistemas ecológicos, los paisajes, diversos recursos, entre otros. Además, como se ha mencionado con anterioridad, los seres humanos ejercemos diversas actividades para mantener, promover o cuidar estos socioecosistemas o recursos. Dichas prácticas han sido registradas a través de un amplio gradiente de actividades de manejo tanto para comunidades vegetales y animales. No obstante, pocos estudios han abordado las prácticas tradicionales que realiza el ser humano con las comunidades microbianas. En este sentido, algunos de los ambientes promovidos por los seres humanos, como es el caso de los productos fermentados, brindan un excelente espacio para abordar el manejo de microrganismos. En la siguiente sección se realizará una descripción general de las prácticas más comunes que se practican para regular o promover el crecimiento de ciertos grupos microbianos, tanto en fermentaciones industriales con un alto nivel de control hasta fermentaciones con un nivel relativamente bajo de control como son las fermentaciones espontáneas.

Hoy en día se practica de manera sistemática la siembra deliberada de algunos microorganismos deseados, que por lo tanto tienen una ventaja selectiva al superar a otros organismos (Figura 1). Este es el caso de las cepas promovidas por las cerveceras, los productores de vino, la industria panificadora, la industria productora de salsa de soya y otros productos que se han industrializado y requieren una homogeneidad en su producción (Parapouli *et al*., 2020). Bajo esta práctica, una de las especies que es frecuentemente utilizada es la levadura *Saccharomyces cerevisiae* la cual tiene una ventaja competitiva debido a su alta capacidad de generar etanol y tolerarlo.

Entonces, podemos decir que las fermentaciones de siembra deliberada son generalmente empleadas con un solo cultivo de cepas que por lo general muestran diferencias significativas metabólicas y biológicas que les dan una ventaja adaptativa sobre otras en la fermentación (Heitmann *et al*., 2018). Cabe señalar que en años recientes el uso de monocultivos en industrias como el vino, el sake, el cacao, entre otros, ha comenzado a repensarse debido a que, si bien garantizan un producto homogéneo, estas otorgan un perfil organoléptico con menor complejidad a comparación de fermentaciones espontáneas o silvestres e incluso al uso de inóculos. Por esta razón en últimos años, se ha comenzado a experimentar con distintos modelos de consorcios microbianos para garantizar productos que sean homogéneos y que tengan una mayor complejidad sensorial (Borren y Tian, 2021).

Tabla 1.- Principales productos fermentados alrededor del mundo, microorganismos asociados y los sustratos con los que se realiza la fermentación

Producto	**Microorganisms**	**Sustrato**
Pan	*Saccharomyces cerevisiae* y distintas levaduras	Harinas de diferentes granos
Fermentaciones vegetales como¨ conservas, pepinillos, aceitunas.	Bacterias ácido-lácticas, *Lactobacillus plantarum, Lactobacillus brevis, Lactobacillus curvatus, Lactobacillus sake, Penicillium* spp., *Leuconostoc mesenteroides*	Diversos productos vegetales
Fermentaciones cárnicas como: Salchichas	*Lactobacilllus bulgaricus*, Pedio cocci, *Saccharomyces xylosus, Meyerozima varians*	Carne de mamíferos, generalmente cerdo o res y con menor frecuencia pollo
Fermentaciones de productos lácticos como: quesos, yogurt	Bacterias ácido-lácticas *Lactobacillus bulgaricus, S. thermophilus, L. shermanii, Penicilliumspp*	Leche, residuos de leche

Datos obtenidos de Lücke 1998, Steinkraus 1997, Caplice y Fitzgerald 1999.

Las fermentaciones realizadas por medio de inóculos o cultivos iniciadores son de los tipos más comunes para elaborar fermentos y son empleados tanto en estado sólido o líquido (Couto y Sanromán, 2016). Este tipo de fermentación implica que los productores decidan deliberadamente tomar consorcios de microorganismos asociadas a fermentaciones previas y emplearlas continuamente en futuras fermentaciones (Figura 1). Es decir, el principio básico es mantener una comunidad estable y constante de microorganismos que permitan obtener un producto homogéneo. Si bien la selección de microorganismos no es dirigida a sus fenotipos, la selección va opera sobre atributos sensoriales y características del producto final. Para ejemplificar, los productores difícilmente asocian atributos favorables del fenotipo como ocurre en plantas o animales, en este caso, se selecciona una fermentación que presentó mejoras en sus atributos sensoriales derivados del metabolismo de los organismos seleccionados, como el color, sabor, textura, acidez, valor nutricional, entre otros, seleccionando así un consorcio de microorganismos que pueden estar involucrados en la fermentación o dependiendo el grado de intensidad del uso del inoculo incluso puede solo seleccionar un linaje microbiano, bacteriano o de levaduras.

Las fermentaciones a partir de inóculos evitan diversas fuentes que pueden agregar variabilidad a las fermentaciones. Por ejemplo, se reduce la variabilidad de microorganismos que pueden provenir del ambiente o de los sustratos animales o vegetales; así mismo, se asume que al ser microorganismos con una mayor especialización en metabolizar los carbohidratos presentes en los sustratos que utilizan para la fermentación, estos ofrecen un mayor rendimiento tanto en el producto como en el tiempo requerido para la producción de estos. La generalidad de este tipo de cultivos es que buscan realizar una fermentación optima en menor tiempo, alcanzar los perfiles sensorialesbuscados por el productor y así replicarlos en las siguientes fermentaciones.

El continente asiático es conocido por sus diversos productos fermentados. Estos son producidos son comunes en países como Japón y China los cuales son elaborados a partir de inóculos.
. Por ejemplo, se llegan a emplear inóculos en estado sólido similares a pastillas o conglomerados secos elaborados de distintas matrices como soya, arroz o trigo son almacenados y utilizados posteriormente como cultivos iniciadores para elaborar productos fermentados como el sake, la salsa de soja u otros. Estos cultivos iniciadores reciben un nombre particular como son el *koji* o el *meji* que son nombres comunes para la producción de sake que tienen como principio fundamental la sacarificación de los azúcares del arroz (Kitamoto *et al*., 2015; Daba *et al*., 2021). Se ha caracterizado que, en estos cultivos, altamente eficientes para la producción, microorganismos como *Aspergillus oryzae* muestra señales de domesticación (Machida et al., 2005; Gibbons *et al*., 2012; Steensels *et al*., 2019). En esta especie se han registrado restructuraciones en distintas regiones del genoma asociadas a cambios en rutas metabólicas y reproductivas a su contraparte y posible pariente silvestre *Aspergillus niger* el cual presenta una mayor presencia de rutas metabólicas asociadas a defensa y patogenicidad (Schuster *et al*., 2002; Watari *et al*., 2019).

Finalmente, la fermentación de tipo espontánea la cual es la forma de fermentación más antigua, en la cual se asume un bajo control y por estos motivos es considerada como inconstante y de baja calidad. No obstante, en la actualidad sigue siendo la práctica de fermentación más común en diversos productos tradicionales (Hesseltine y Wang 1976; Campbell-Platt, 1994; Tamang, 1998; Kabak y Dobson, 2011). Básicamente la fermentación espontánea ocurre con las comunidades de

microorganismos asociados a los sustratos, que pueden ser de origen animal o vegetal. Es importante señalar que dentro de estas fermentaciones hay una reducción de la variabilidad ambiental que puede darse en ambientes naturales, es decir los ambientes fermentativos promovidos por el ser humano, ya sea en ollas, cajones, u otros contenedores, reduce la heterogeneidad del ambiente y hay una ligera homogeneización tanto del sustrato, como de la variación ambiental (Gibbons *et al*., 2012; Gibbons y Rinker, 2015; Gibbons, 2019). En estas fermentaciones se ha registrado una amplia gama de especies de bacterias y levaduras, particularmente, en etapas iniciales de la fermentación (Gibbons *et al*., 2012; Cheeseman *et al*., 2014; Gibbons y Rinker, 2015; Gibbons, 2019; Dumas *et al*., 2020). Al mismo tiempo, un factor clave dentro de estas fermentaciones son las condiciones de procesamiento, las cuales son clave pues pueden permitir el ingreso de otros microrganismos, es decir, el transporte de lasmaterias primas, las herramientas utilizadas, o incluso el ambiente y el espacio físico en donde fueron procesados.

Estas prácticas de fermentación han sido evaluadas en la elaboración del cacao y el café que involucran fermentaciones espontáneas. En estos productos se ha registrado una alta diversidad de levaduras en las etapas iniciales de la fermentación la cual promueve la formación de una amplia gama de productos metabólicos finales, como alcoholes, ácido acético y otros ácidos orgánicos, que se difunden en los granos y en la pulpa (Borren y Tian, 2021). Así, se inducen transformaciones bioquímicas dentro de los granos que conducen a la formación de precursores de aromas, sabores y colores característicos, que se desarrollan aún más durante el secado y finalmente se obtienen durante el tostado y el procesamiento posterior (Schwan y Wheals 2004; Jespersen *et al.,* 2005). En general, en los últimos años el manejo de las fermentaciones han comenzado a tomar una importante relevancia debido a la alta diversidad de microorganismos presentes y debido a las aplicaciones biotecnológicas de estos grupos. Por ejemplo, en la industria vitivinícola se busca mantener vinos silvestres que involucran fermentaciones espontáneas con la microbiota asociada a los viñedos, para ofrecer un sello único en el producto final conocido como terruño o *terroir* en el francés.

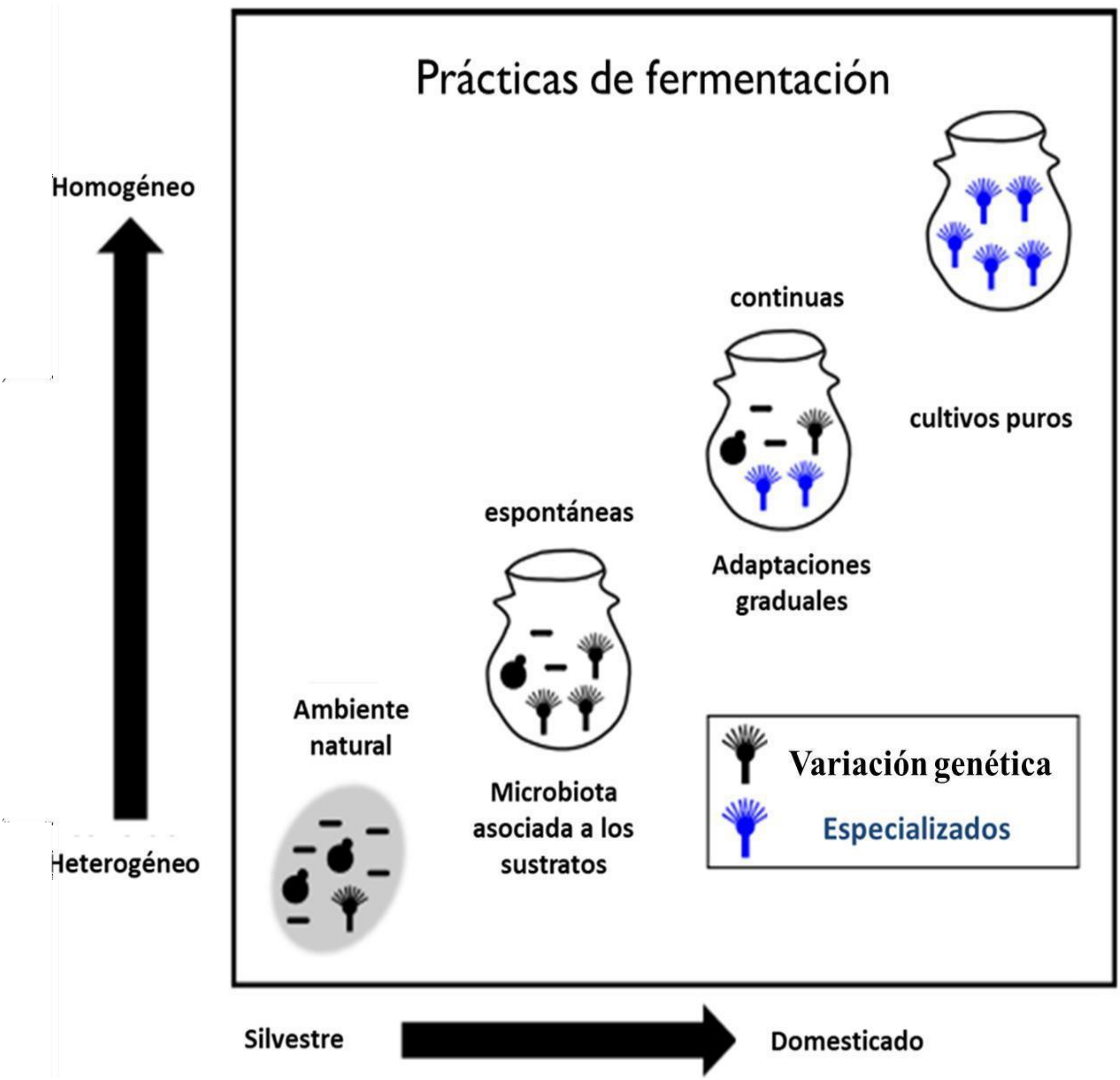


Figura 1.- Esquema general de las tipologías de prácticas de fermentación (Gibbons y Rinker, 2015), el gradiente de domesticación que estos microorganismos presentan y el grado de heterogeneidad promovida por los productores de fermentos. En la parte inferior izquierda se puede ver que los microorganismos se encuentran en condiciones bajo una alta heterogeneidad ambiental en donde la competencia es mayor y no se realiza una selección de microorganismos. Posteriormente, en las fermentaciones espontáneas ocurre una reducción de esta variabilidad ambiental y una selección de microorganismos asociados a las materias primas, ya sean de origen vegetal o animal. En fermentaciones continuas o por inóculos ocurre que se adicionan consorcios de microrganismo usados en fermentaciones previas a fermentaciones que ocurrirían espontáneamente. El constante uso de estos consorcios promueve que algunos se encuentren especializados a estas fuentes de carbohidratos que en algunos casos suelen ser específicos. Finalmente, como se mencionó en el texto la presencia y el uso de organismos especializados en fermentaciones que son elaboradas a partir de cultivos puros, como esel caso de la mayoría de las fermentaciones a nivel industrial.

Prácticas empleadas en el manejo de las fermentaciones

Arriba se mencionaron los tres tipos generales de fermentación, desde las fermentaciones “rústicas” y fermentaciones más tecnificadas, hasta un extremo de la especialización del uso de monocultivos. Algo similar ocurre en términos de los recursos vegetales y animales, en donde se encuentra la recolección como la práctica más básica, a la agricultura o en el caso de animales de la casería a la ganadería (Casas *et al*., 2016). Si bien estas prácticas representan los extremos del manejo de recursos, existen variaciones dentro de cada tipología que producen cambios en la intensidad del manejo. Entonces se entiende como a la intensidad de manejo como una relación del grado de especialización o complejidad de las prácticas realizadas, el número de prácticas que se ejercen y el número de personas que realizan dichas prácticas (Gonzáles-Insuasti y Caballero, 2007). Además, estas pueden verse en función de distintas características como: la energía invertida en el sistema (mano de obra).La complejidad de las herramientas, técnica y estrategias utilizadas. En el caso de las fermentaciones los contenedores de la fermentación son muy diversos, pues estos pueden ir desde fermentadores industriales de acero inoxidable y con capacidades de controlar la temperatura, hasta ser intestinos de animales donde la fermentación puede llevarse a cabo. La cantidad de productos obtenidos porproducto manejado (Altieri y Koohafkan, 2004, Casas *et al*., 2008, Blancas *et al*., 2010) Esto puede verse en el caso de fermentaciones industriales en donde la tecnología para elaborar la fermentación reduce dramáticamente el tiempo de producción incrementa los volúmenes de producción. Como podemos ver, en el caso de comunidades de microorganismos asociados a espacios fermentativos esta intensidad de manejo no es ajena, pues el productor ejerce distintos procesos que generan cambios en la microbiota de estos ambientes.

Una de las prácticas empleadas comúnmente en etapas previas o durante la fermentación es el uso de tratamientos físicos o químicos los cuales pueden tener implicaciones significativas en la dinámica de la fermentación. Comúnmente, en los productos alimenticios el cambio de temperatura es un tratamiento frecuente y se emplea en los distintos tipos de fermentación. Esta puede emplearse como calor húmedo que involucra vapor de agua a alta presión, el cual es altamente eficaz para esterilizar materiales, los sustratos o los contenedores donde se realiza la fermentación (Lopez-Castrillon *et al*., 2018). Igualmente se puede emplear calor seco para la esterilización de materiales, el cual puede ser más tardado y menos efectivo con algunos materiales. El uso de calor seco en las deshidrataciones o en el caso de la panificación el principio reduce la comunidad previa a la fermentación, limitando el acceso al agua y promueve el crecimiento de un cierto grupo de especies que toleraran esta temperatura y la baja disponibilidad de agua. En el caso de fermentaciones industriales se realizan tratamientos de ultra alta temperatura en donde se garantiza la ausencia de microorganismos ajenos para realizar fermentaciones homogéneas (Bahrami *et al.*, 2020).

Un caso más conocido que involucra el cambio en la temperatura es la pasteurización. Este tratamiento es en cierto grado menos drástico a una esterilización, pues el tiempo de exposición y la temperatura es controlada y no se afecta tan negativamente las propiedades finales del producto, pero se logra la eliminación de microorganismos nocivos. Este proceso favorece mantener cierto grupo de microorganismos, mayoritariamente benéficos y reducir a los posibles patógenos o letales, es una práctica común para diversos productos de origen láctico y también para otros productos industriales como es el caso de algunas cervezas (Anderson, 2019; Dhar *et al.*, 2022). Así mismo, la reducción de la temperatura juega un papel clave en la producción de algunos productos fermentados ya que reduce la capacidad de crecimiento de algunos organismos. Por ejemplo, en la industria vitivinícola esta práctica se emplea para promover el crecimiento de levaduras que no pertenecen al grupo de *Saccharomyces*. Al reducir la temperatura debajo del óptimo de crecimiento de *Saccharomyces* otras cepas pueden proliferar y la competencia se reduce. De hecho, esta práctica promueve el desarrollo de un perfil sensorial complejo y una menor concentración de etanol, como ocurre en algunos vinos de regiones frías (Luan *et al.*, 2018; Johnson et al., 2020). De igual manera, la congelación es una práctica común para mantener los productos con un tiempo de anaquel más largo, debido a lareducción de crecimiento de microorganismos, un ejemplo particular es el que ocurre en las montañas de la región Aimara del Perú, en donde papas u otros tubérculos son deshidratados y liofilizados en zonas de montañas altas y posteriormente son utilizados para producir un platillo conocido como chuño (Márquez Mendoza, 2019).

Otra práctica que ocurre previo a la fermentación es el secado de los sustratos. El secado permite la conservación de sustratos tanto animales (pescado) como vegetales (cereales y frutas) y permite almacenar estos sustratos satisfactoriamente previo a su uso (Doe y Olley, 2020). El principio del secado es reducir la disponibilidad del agua para el metabolismo microbiano. Además, esta práctica es comúnmente acompañada con la adición de solutos como sal o azúcar, esta acción es deliberada en muchos productos para lograr la conservación de los alimentos (Fraqueza *et al.*, 2021). La alta concentración de sal limita el crecimiento de un amplio espectro de microorganismos y solamente las especies tolerantes a ambientes halófilos pueden mantenerse (Elias e*t al.*, 2020). Recientemente se ha registrado que las bacterias asociadas a estos ambientes presentan una gran capacidad de desarrollar rutas metabólicas de defensa asociadas a la producción de bacteriocinas que también juegan un papel clave en la competencia con otros microorganismos y de una amplia utilidad biotecnológica (Chhetri *et al.*, 2019). Este tipo de prácticas se observa comúnmente para la elaboración de pescado fermentado, embutidos y salmueras. En el caso del azúcar ocurre un efecto similar, la alta concentración de azúcares no permite el desarrollo de la mayoría de los microorganismos, estos productos pueden verse como el caso de mermeladas o conservas (Mani, 2018).

En las instalaciones modernas de producción de alimentos, el uso de agentes químicos para limpiar fácilmente las instalaciones de producción, las herramientas, los materiales plásticos, los fermentadores, incluso en los insumos se ha convertido en una práctica habitual. A grandes rasgos se busca que el agente químico llegue a todos los rincones y espacios para eliminar posibles contaminaciones (Alfarobbi y Anggraini, 2018). Por lo general los protocolos industriales emplean detergentes para el lavado y una posterior esterilización u otros compuestos como es el dióxido de cloro o ácido peracético, entre otros. No obstante, en la mayoría de las fermentaciones tradicionales el uso de agentes químicos no es común. Sin embargo, durante las fermentaciones "rústicas" los fermentadores tradicionales emplean algunos productos como cortezas de árboles, cascaras de vegetales, entre otros productos que contienen compuestos antimicrobianos naturales como como bacteriocinas o la nicina, u otras especies vegetales que contienen polifenoles, o en el caso de la producción de salmueras se utiliza de ácido acético el cual es especialmente importante para contrarrestar el crecimiento de bacterias, levaduras y mohos (Joardder y Masud, 2019).

Como se mencionó en el párrafo anterior, en las fermentaciones tradicionales los productores deciden deliberadamente agregar productos que muchas ocasiones regulan o favorecen a ciertosgrupos microbianos. Asimismo, se llega a emplear otros productos que mejoren o favorezcan la velocidad de la fermentación y son conocidos como aditivos o fortalecedores. A nivel industrial esto también ocurre, por ejemplo, al agregar lúpulo en la fermentación de cerveza no solo altera los atributos sensoriales de una cerveza, sino que durante la fermentación ocurre la producción de los iso-α-ácidos, que son clave en la protección de la fermentación y evitan el deterioro de la bebida (Bocquet *et al.*, 2018; Yan *et al.*, 2019). Particularmente, en los productos fermentados tradicionales o de baja escala el uso de aditivos y otros productos antisépticos han sido muy pocas veces considerado en los estudios de fermentaciones.

No obstante, se ha documentado que para la producción de bebidas fermentadas se utiliza la canela (*Cinamomum verum*) o el anís estrellado (*Illicium verum*) y el jengibre(*Zingiber officinale*), no solo para dar distintos sabores a la bebida, sino, que también tienen propiedades antisépticas que controlan la comunidad de microorganismos o en el caso de una bebida fermentada mexicana conocida como tejuino la cual tiene de base el maíz se utiliza un moho como fortalecedor. En el caso de fermentaciones vegetales, como la col fermentada y en una amplia gama de salmueras, se utiliza la pimienta (*Piper* spp), el clavo (*Syzygium aromaticum*), o el comino (*Cuminum cuminum*) como fortificadores en estas fermentaciones.

Los productos fermentados en esencia son sistemas dinámicos, con interacciones pocas veces estudiadas. Suelen ser muy variables en el caso de las fermentaciones tradicionales en donde cada producción lleva diversos cambios que pueden alterar el resultado final del producto y su estudio resulta complejo. No obstante, podemos decir que el ser humano ejerce diversas prácticas en distintas escalas y en diferentes intensidades que se realizan previo, durante o posterior a la fermentación, y estas actividades ocurren tanto en las fermentaciones más rusticas como en las más industrializadas. Los motivos son diversos, como alcanzar sabores, texturas, olores, entre otros, pero estas prácticas tienen diversas implicaciones como cambios en el pH, el contenido de ácidos orgánicos, el contenido de etanol, el dióxido de carbono, la actividad del agua, entre otros factores que modifican la comunidad microbiana y su dinámica (Panghal *et al*., 2018). En general, podemos decir que existen diversas prácticas e intensidades de manejo sobre comunidades de microorganismos en la elaboración de productos fermentados, haciendo que la producción de estos resulte en un complejo gradiente de conocimientos tradicionales para elaborar estos productos. Igualmente, se puede añadir que muchas deestas prácticas o implicaciones que realizan los productores no se han abordado y existe una amplia laguna de información que puede aportar a una teoría robusta del manejo y particularmente al manejo de microorganismos, así como, de conocimientos que pueden emplearse en diversas aplicaciones.

Productos fermentados tradicionales: la efervescencia dentro de la alimentación local

A nivel doméstico y local diversos alimentos y bebidas fermentados tradicionales se producen alrededor del mundo (Campbell-Platt, 1994; Panghal *et al*., 2018; Roig-Coll y Kechagia, 2020). De hecho, existen productos cuya materia prima puede llegar a ser venenosa o contener productos que puedan no ser sencillamente digeribles por los seres humanos y el proceso de transformación que ocurre durante la fermentación permite que estos productos que pueden ser nocivos o no viables parael consumo humano puedan incorporarse en la dieta, tal es el caso de la fermentación de la yuca (*Manihot utilissima*), que al pasar por la fermentación se obtiene un producto libre de cianuro y puede ser incorporado como alimento seguro en la dieta (Liener, 1969, 1976). Estas fermentaciones domésticas son relevantes porque no solo proporcionan importantes fuentes de nutrientes o un métodoeconómico para darle un mayor tiempo de vida a los productos, sino que también tienen un gran potencial para mantener la salud y prevenir enfermedades (Manning *et al*., 2019). Es importante señalar que en muchos de estos productos se han caracterizado microorganismos como bacterias del ácido láctico y las levaduras con potenciales beneficios a la salud, a nivel local son utilizados como remedios medicinales para combatir enfermedades gastro intestinales diarreas o en general fortalecer el sistema inmune (Kehinde *et al.*, 2020; Zandona *et al*., 2020; Łopusiewicz *et al*., 2021).

Son considerados como productos tradicionales todos aquellos alimentos elaborados bajo las siguientes consideraciones (Guerrero *et al.,* 2009): 1) Los pasos clave de producción se deben realizar en un área nacional, regional o local determinada, (2) el alimento tradicional puede ser auténtico en su receta, origen de la materia prima y/o proceso de producción, herramientas, (3) el producto debió haber sido intercambiado localmente durante varios años, disponible a menudo a través del trueque o solo consumido por el núcleo familiar, y (4) es considerado por la comunidad como parte delpatrimonio gastronómico local o nacional. Sin embargo, se ha reconocido que los productos tradicionales son dinámicos, el ambiente proporciona los materiales (sustratos crudos y herramientas) que permiten a los grupos enraizarse en su pasado y moverse y al mismo tiempo la extraordinaria capacidad de experimentación por parte del ser humano permite reconstruirse en el presente (Gellyncky Kühne 2008; Guerrero *et al*., 2009; Kühne *et al*., 2010; Gallager y McKevitt, 2019).

Ensambles microbianos: los lauderos del sabor y los sonidos de su interacción

Como se ha ido desarrollando en las secciones anteriores, uno de los aspectos clave en todas las fermentaciones son los microorganismos, estos agregan valor y mejoran la calidad nutricional, la digestibilidad a través del enriquecimiento biológico, y proporciona un enriquecimiento sensorial a los productos a través de la producción de aromas y sabores y la modificación de las texturas de los diversos sustratos alimentarios con los que se elaboran. Este numeroso e imperceptible grupo de organismos es el responsable de descomponer los carbohidratos complejos y las proteínas en elementos fácilmente digeribles. Los microorganismos más comunes dentro de las fermentaciones pueden dividirse a grandes rasgos en dos categorías: los procariotas y los eucariotas. Los primeros, que abarcan a las bacterias, son relativamente más simples, ya que esencialmente comprenden una pared celular protectora la cual juega un papel clave para la determinación e identificación de estos grupos, esta rodea una membrana plasmática, dentro de la cual hay una región nuclear inmersa en el citoplasma. En el citoplasma se encuentran las enzimas que catalizan las reacciones necesarias para el crecimiento, supervivencia y reproducción de los organismos, es decir su metabolismo. A través de su membrana se regula la entrada y salida de materiales dentro y fuera de la célula. Esta es unadescripción algo simplista, pero suficiente para describir las necesidades de la presente tesis.

Por otro lado, las células eucariotas, como las de las levaduras y hongos, son sustancialmente más complejas (Kurtzman y Fell, 1998). Esta presenta distintos orgánulos, cada uno con diferentes capacidades para realizar funciones específicas, el material genético se ubica en el núcleo el cual está delimitado por una membrana como la mayoría de los orgánulos. Las mitocondrias son los orgánulos donde se genera energía, y el retículo endoplásmico es una red interconectada de túbulos, vesículas y sacos con diversas funciones que incluyen la síntesis de proteínas, el secuestro de calcio, la producción del glucógeno y la inserción de proteínas en las membranas. Particularmente el hongo unicelular más importante pertenece a *Saccharomyces* (Kurtzman, 2011). Sin embargo, los hongos filamentosos con sus hifas (mohos), son importantes para varios productos alimenticios, en particular los productos asiáticos que implican fermentaciones en estado sólido, como es el caso del sake (una bebida fermentada y destilada elaborada a partir de arroz) y miso (una pasta fermentada elaborada a partir de soja).

Dominio Bacteria

Las bacterias son organismos procariotas unicelulares, que se encuentran distribuidos en casi todas las partes de la Tierra. Son vitales para los ecosistemas del planeta. Algunas especies pueden vivir bajo condiciones realmente extremas de temperatura y presión. El cuerpo humano está lleno de bacterias y, de hecho, se estima que contiene más bacterias que células humanas (Turnbaugh *et al*., 2007). La mayoría de las bacterias que se encuentran en el organismo no producen ningún daño, solo una cantidad relativamente pequeña de especies son las que causan enfermedades. Algunas son beneficiosas, incluso en la actualidad se recomienda la ingesta de estos grupos benéficos provenientes de productos

fermentados (Zmora *et al.*, 2016; Wilson *et al.*, 2020; De Filippis *et al.*, 2020). Las bacterias al ser el grupo más diverso y aún el más desconocido por el ser humano tiene complicaciones para su clasificación e identificación. No obstante, en la actualidad el uso de secuencias del gen 16S rRNA permite estudiar la filogenia y la taxonomía bacterianas y es elmarcador genético más común utilizado por varias razones (Balcázar *et al.*, 2007). Por ejemplo, (i) su presencia se encuentra conservada en casi todas las bacterias, a menudo existiendo como una familia multigénica u operones; (ii) la función del gen 16S rRNA a lo largo del tiempo no ha cambiado, lo quesugiere que los cambios de secuencia aleatorios son una medida más precisa del tiempo (evolución); y
(iii) el gen 16S rRNA (1500 pb) es lo suficientemente grande para fines informativos. Además, este marcador, acoplado a técnicas modernas de secuenciación, ha disparado el número de especies conocidas en los años ochenta que eran 1.791 a 8.168 especies reconocidas en la actualidad (Youssef et al., 2015).

Un grupo clave en los alimentos y bebidas fermentadas son las bacterias ácido-lácticas, las cuales han sido descritas en diversos productos de fermentaciones lácticas y alcohólicas de distintos productos vegetales o animales. Las bacterias del ácido láctico (LAB por sus siglas en inglés)generalmente son reconocidas como microorganismos seguros e involucran un amplio número de especies que tienen una diversa gama de aplicaciones industriales, como la fermentación de alimentos, la producción de fármacos, química y otras aplicaciones industriales, (Jabłońska-Ryś *et al.*, 2019; VanTilburg *et al.*, 2019; Venegas-Ortega *et al.*, 2019). Durante los últimos años, la aplicación más destacada de este grupo de bacterias es como cultivos iniciadores para la producción de alimentos fermentados, donde estas contribuyen a las propiedades finales organolépticas, nutricionales y saludables de los alimentos fermentados (Gao *et al.*, 2021; Shafi *et al.*, 2014; Wu, Huang y Zhou, 2017). Los cultivos iniciadores de LAB generan un entorno bacteriostático o incluso bactericida al reducir el pH de la matriz alimentaria para evitar el deterioro de los productos y las bacteriaspatógenas que compiten por el nicho ecológico durante la fermentación del ácido láctico no pueden establecerse. Además, a la fecha se reconoce que algunos genomas de bacterias ácido-lácticas se han simplificado debido a una adaptación a los ambientes alimentarios ricos en nutrientes en donde se mantiene una baja competencia (Sun *et al.*, 2015). Este proceso evolutivo a conducido a la simplificación metabólica en el genoma de este grupo de bacterias, lo que ha resultado tanto en múltiples deficiencias nutricionales debido a la pérdida de varias vías biosintéticas, así como a la especificidad a ciertas fuentes de carbono (Douglas y Klaenhammer, 2010; Bachmann *et al.*, 2012; Bull *et al.*, 2014, Steensels *et al.*, 2019).

Las LAB se clasifican taxonómicamente como homofermentativas, heterofermentativas facultativas y heterofermentativas dependiendo de su principal metabolismo de carbohidratos (Ganzle 2015), dependiendo de la función principal de estas bacterias en los alimentos fermentados es transformar los carbohidratos en ácido láctico acidificando así rápidamente la matriz alimentaria, evitando así que organismos patógenos proliferen o que el deterioro por parte de otros organismos se vea limitado, a grandes rasgos este ambiente fermentativo genera restricciones para algunos organismos y ventajas para otros. Además, algunas especies de este grupo de bacterias puedencontribuir a la formación de sabores únicos en los alimentos fermentados. Los géneros más comunes de bacterias ácido-lácticas en alimentos fermentados son *Lactobacillus*, *Leuconostoc*, *Weissella*, *Lactococcus*, *Streptococcus*, Enterococcus, *Pediococcus*, *Oenococcus*, *Carnobacterium* y *Tetragenococcus* (Papadimitriou *et al*., 2016; Zheng *et al*., 2020). En la actualidad distintos de estos géneros están siendo estudiados debido a que son consideradas como microorganismos con potencial probiótico y sin duda son parte de las tendencias biotecnológicas de los últimos años. Así mismo, la velocidad y la confianza de la secuenciación de este grupo microbiano han permitido monitorear la calidad de alimentos y bebidas, garantizando así la seguridad para su ingesta (Soomro *et al*., 2002; Quinto *et al*., 2015).

Levaduras

Las levaduras son hongos unicelulares ascomicetos o basidiomicetos que se reproducen vegetativamente por gemación o fisión, y que forman estados sexuales que no están encerrados en un cuerpo fructífero (Boekhout y Kurtzman, 1996). Las subdivisiones se basan en aspectos de la sexualidad de las levaduras Ascomycotina (presencia de Ascas) o Basidiomycotina (presencia de Basidios) o la falta de ella (Deuteromycotina). Particularmente, el hecho de que este grupo sea diversocomplica la identificación certera de especies. No obstante, para precisar la categorización taxonómica, también se emplean varias características morfológicas, fisiológicas y genéticas (Barnett, 1992). Actualmente, a través de métodos independientes del cultivo, conlos cuales el ADN es aislado directamente de muestras ambientales ya sea de alimentos o bebidas fermentadas, se utilizan diversos marcadores moleculares como el de la región espaciadora interna transcrita del ADN ribosomal (ITS) amplificados mediante la reacción en cadena de la polimerasa (PCR por sus siglas en inglés), para detectar tanto levaduras ascomicetos o basidiomicetos a través de tecnologías como la secuenciación de nueva generación (SNG) (Cuadros-Orellana, 2013). Estos marcadores tienen la resolución suficiente para el nivel de especie para diversos hongos y discrimina el ADN de plantas (Gardes y Bruns, 1993, Schoch *et al*., 2012), permitiendo así un gran avance para la identificación y un mayor registro de hongos (Fajarningsih, 2016; Xu, 2016; Truong *et al.*, 2017). De forma complementaria, se realizan métodos dependientes de cultivos en medios artificiales, de los cuales se puede analizarciertas secuencias o genomas completos y se realizan caracterizaciones fenotípicas para clasificarlos (Gibbons y Rinker, 2010, 2015; Dujon, 2010; Kurtzman, 2011). Ambos métodos combinados permiten establecer un sistema taxonómico confiable como base para la identificación (Mortirmer, 2000; Cherry *et al.*, 2012; Engel *et al.*, 2021).

Las levaduras tienen un enorme impacto en la producción de diversos alimentos y bebidas, sin embargo, la comprensión científica y tecnológica de sus funciones comenzó relativamente tarde. Los primeros estudios surgieron a mediados del siglo XIX por Pasteur en Francia y Hansen en Dinamarca sobre la microbiología de la cerveza y el vino, abriendo así los inicios de disciplinas como la microbiología y la bioquímica. Desde entonces las personas alrededor de todo el mundo, ya sea que tengan formación científica o no científica, se han embarcado en un mundo de descubrimientos y desarrollos tanto de alimentos y bebidas fermentadas, aprendiendo y diversificando productos que son transformados a partir de la actividad de un amplio número de levaduras y sus también diversos mecanismos bioquímicos, fisiológicos y moleculares que sustentan las numerosas funciones de las levaduras como su utilidad en la producción de combustibles, enzimas, proteínas, lípidos y pigmentos (Hittinger *et al.*, 2015). Históricamente han revolucionado el mundo debido a su gran utilidad y han permitido formar grandes industrias como la cervecera y la vinícola, así como otras industrias.Además, en los últimos años los datos genómicos provenientes de diversos productos o ambientes hanpermitido, entrever procesos evolutivos, mecanismos adaptativos, diversidad genética y metabólica. Especialmente, *Saccharomyces cerevisiae* se ha convertido en uno de los sistemas modelo favoritos para genetistas, ecólogos y biólogos evolutivos interesados en diversos aspectos biológicos de los eucariotas y aplicaciones biotecnológicas (Douglas y Klaenhammer, 2010).

Es claro que no se puede estudiar la complejidad intrínseca de las levaduras únicamente a través de *S. cerevisiae* y menos cuando la mayoría de los estudios son realizados bajo condiciones controladas en el laboratorio. Es importante considerar a las levaduras como sistemas abiertos que interactúan con diversos factores tanto bióticos como abióticos y en este sentido las fermentaciones y las tradicionales son espacios idóneos para el estudio de estas. Lamentablemente, la gran mayoría de los estudios de levaduras se ha dirigido al estudio de levaduras en condiciones controladas y en menor grado a casos como fermentaciones tradicionales. Esto, sin mencionar la escasez estudios que involucren el uso de levaduras no pertenecientes al género *Saccharomyces*. Al tratar de estimar el número de especies de levaduras existentes, generalmente se llega a la conclusión de que, al igual que otros grupos de microorganismos, una proporción muy pequeña de las levaduras, posiblemente solo el 1% de las especies, se han descrito. Los estudios de la diversidad de levaduras se han centrado principalmente en inventarios taxonómicos, con énfasis en la descripción de especies nuevas y las descripciones parten únicamente de una sola cepa. Esto es una gran laguna de investigación pues la información aún falta o se mantiene incompleta (Kurztman, 2011).

En años recientes, se ha estudiado un creciente número de hábitats en donde se han identificado a través de medios de cultivo y medios independientes del cultivo un mayor número de levaduras; así mismo, se ha caracterizado una mayor cantidad de información ecológica y la biología de estas especies. La combinación de tecnologías de secuenciación con el apoyo de marcadores moleculares, y los avances conceptuales en estadística y sistemática, permiten que estas comunidades puedan ser analizadas con una mayor robustez. Particularmente, en los últimos años el avance conceptual ecológico de los números de diversidad de Hill ha permitido que el análisis de estas comunidades sea similar al de comunidades biológicas a nivel macro (Chao *et al.*, 2010, 2012, 2014), permitiendo así explorar la complejidad ecológica de estas micro comunidades.

El triángulo diversificador: plantas grupos culturales-microorganismos

La selección natural promueve una amplia diversidad de los grandes grupos microbianos de los que aún poco sabemos, pero podemos intuir que bajo condiciones naturales se enfrentan diversas condiciones agrestes e incluso condiciones ambientales inimaginables para la sobrevivencia de otros organismos, como puede ser el fondo marino, pozas termales, entre otros (Kristjansson y Hreggvidsson, 1995; Gupta *et al.*, 2014; Daoud y Ali, 2020). Asimismo, la selección artificial que se ejerce en estas comunidades es un proceso diversificador de los sistemas biológicos a distintas escalas de organización, ocurren continuamente y además proveen recursos genéticos que son útiles para distintas aplicaciones (Leducq *et al.*, 2014; Gibbons y Rinker 2015; Hittinger *et al.*, 2018). En el caso de los microorganismos de productos fermentados responden también a continuos cambios culturalesy a procesos altamente dinámicos que impulsan nuevas necesidades socioculturales en el mundo contemporáneo, como es el satisfacer la demanda de alimentos.

Es necesario y útil analizar cómo ocurren tales procesos en diferentes contextos: tanto entre los sectores rurales como entre los industriales, pues en todos ellos opera la domesticación impulsada por culturas, economías y ambientes de distinta índole, en diversos escenarios socioecológicos. Estos contextos son interesantes no solo por la antigüedad de su historia, la cual permite estudiar los procesos que condujeron al origen de la agricultura, así como a una detallada producción de fermentos, y a la alta diversificación de recursos genéticos que puede documentarse en ellas (Casas *et al*., 2007; Aguirre-Dugua *et al*., 2012; Parra *et al*., 2010, 2012). En los hogares de distintas regiones del mundo siguen vigentes distintos procesos de domesticación que involucran una alta diversidad biocultural, y que son invaluables para entender la diversidad de procesos antiguos y actuales que han intervenido en la modelación de la diversidad de los recursos genéticos que se encuentran disponibles alrededor del mundo. Entender la relación entre los seres humanos, las plantas que utilizan para realizar productos fermentados y los microorganismos involucrados brinda la oportunidad de conocer la variedad de causas que influyen en los procesos de manejo y domesticación de recursos genéticos, las rutas que estos adoptan, sus resultados y perspectivas (Casas *et al*., 2007, 2015; Aguirre-Dugua *et al*., 2012; Parra *et al*., 2010, 2012).

La domesticación no solo incluye a organismos que forman poblaciones biológicas, también es un proceso que opera adecuando a las comunidades bióticas, los ecosistemas, los paisajes o los micro paisajes que el ser humano promueve a través de la elaboración de productos fermentados, así como en los territorios conforme a los intereses y deseos humanos. Domesticar es un término que deriva de la palabra latina *domus* que significa "casa", y puede incluir también los significados de "llevar a la casa", "incorporar a la casa" o "construir la casa"; todos estos significados, en especial el de la construcción de la casa, significa *sensu stricto* adecuar el mundo circundante de acuerdo con los requerimientos de los grupos humanos que lo habitan. A grandes rasgos, la domesticación no puede definirse como un fenómeno biológico o cultural, más bien como un mutualismo biológico transformado por la capacidad humana (Odling- Smee, 1996, Terrell *et al.*, 2003; Staller, 2006, Zeder, 2006; Kendall *et al.*, 2011, Zeder, 2015). El estudio de la domesticación de microorganismos es relativamente nuevo y sin duda estudiarlos a través de la producción de fermentos, permite vislumbrar estas rutas de construcción deliberada de espacios generados por los humanos y los recursos naturales vivos y no vivos que son componentes clave en la alimentación y en la cultura.

La mayoría de los estudios de microorganismos en alimentos fermentados se ha dirigido a aquellos de relevancia económica para el mercado capitalista como el pan, vino, cerveza y diversos productos lácticos. No obstante, los productos fermentados producidos a menor escala son la base económica y alimenticia para muchos consumidores en países subdesarrollados o en vías del desarrollo. Además, es la forma más económica de conservar los alimentos y en algunas regiones es laúnica (Tamang, 2009; 2010; Hittinger *et al*., 2016). Es particularmente importante señalar que cada comunidad en el mundo tiene una cultura alimentaria distinta, incluidos los alimentos y las bebidas fermentadas, que simbolizan el patrimonio y los aspectos socioculturales de las comunidades. Estos espacios alimentarios también representan una amplia diversidad de microorganismos (Tamang y Fleet 2019; Tamang *et al*., 2016). Sin embargo, el consumo de alimentos fermentados menos conocidos y poco comunes está disminuyendo debido al cambio en los estilos de vida que está pasando de hábitos alimentarios culturales a alimentos comerciales y a la industria de comidasrápidas. Entre otros, estos factores afectan drásticamente las prácticas culinarias tradicionales, y junto con otros procesos que influyen en el cambio global, ponen en riesgo la permanencia de estosproductos en los paisajes alimentarios y a los microorganismos asociados como parte de esta diversidad biológica pocas veces considerada.

El propósito del presente estudio es mostrar y ampliar de manera sistemática la información disponible de los productos fermentados tradicionales de México, y particularmente profundizar en una bebida fermentada poco estudiada, el colonche. Se pretende realizar aportes conceptuales a los procesos del manejo y domesticación para el caso de comunidades de microorganismos y enfatizar en la importancia que estos productos tienen como espacios de diversificación, de identidad y a nivel nutricional. Finalmente, aportar información que permita desarrollar una estrategia de conservación de las bebidas fermentadas tradicionales. La investigación está dirigida a contestar las siguientes preguntas: ¿Qué diversidad bio-cultural albergan las bebidas fermentadas tradicionales?, es decir, la riqueza de especies de plantas, grupos culturales y microorganismos involucrados en su producción ¿Qué procesos y prácticas se realizan para la elaboración de una bebida fermentada tradicional elaborada a partir de frutos de cactáceas ¿En qué medida afectan las prácticas de manejo empleadas por los productores a la estructura, composición y diversidad de la comunidad de microorganismos asociadas a un producto fermentado tradicional?

Hipótesis

Las bebidas fermentadas tradicionales de México son el resultado de la síntesis de una gran diversidad biológica y cultural. En tal contexto, esperamos identificar una alta diversidad de productos relacionada con la diversidad cultural igualmente alta representada por la cantidad de grupos indígenas que se distribuyen a lo largo de las diferentes regiones y ecosistemas de México. En particular, al analizar el caso del fermento conocido como colonche, esperamos que se presenten cambios en la comunidad de microorganismos dependiendo de las prácticas de manejo en la fermentación. Las formas de manejo de fermentación espontánea incluirán la mayor diversidad de las comunidades de microorganismos, mientras que las diferentes técnicas asociadas a la inoculación o búsqueda de atributos especiales determinarán una menor diversidad, exacerbando la abundancia de algunos grupos de organismos relacionados con tales atributos.

Objetivo general

Caracterizar las bebidas fermentadas tradicionales fermentadas en el contexto de la diversidad biocultural de México, los sustratos vegetales empleados, los grupos culturales y los microorganismos reportados en la literatura. Así mismo, detallar los procesos en la producción de una bebida fermentada tradicional mexicana (el colonche), elaborada a partir de frutos de cactáceas y evaluar las implicaciones que tienen las prácticas de manejo en la microbiota.

Objetivos particulares

- Identificar las bebidas fermentadas en el país, el estado del arte sobre la investigación de este grupo de productos a nivel nacional. De igual manera, registrar el número de sustratos vegetales, grupos culturales y microorganismos caracterizados en su producción, y registrar su distribución geográfica en el país.
- Documentar el proceso de elaboración del colonche, una bebida fermentada elaborada a partir de frutos de cactáceas, registrar los sustratos utilizados en su producción, caracterizar las prácticas de manejo de microorganismos para la fermentación y identificar los factores socio-culturales de los productores.
- Identificar las implicaciones del manejo en las fermentaciones en la comunidad de microorganismos. Identificar cambios en la riqueza, diversidad y dominancia de hongos y bacterias bajo las prácticas de fermentación espontánea e inoculación en el colonche.

Las preguntas, hipótesis y objetivos de esta investigación se abordaron analizando el contexto general de las bebidas fermentadas tradicionales de México, su diversidad y distribución. Se centró la atención en un grupo de bebidas conocidas como “colonche” para detallar aspectos de su manejo y posteriormente se analizó la estructura de las comunidades de microorganismos en relación con un tipo de colonche preparado en el Altiplano Central de México con *Opuntia streptacantha*. La Tesis presenta tres capítulos principales. El primero de ellos se titula: “Traditional Fermented Beverages of Mexico: A Biocultural Unseen Foodscape”. Es un artículo de revisión el cual se presentó en el foro de la revista *Foods* tuvo como principal objetivo documentar la diversidad de bebidas fermentadas tradicionales en el país, las tendencias de investigación sobre estos productos, los recursos vegetales utilizados, los grupos culturales asociados a la producción y los microorganismos hasta ahora documentados para las distintas bebidas.

México es reconocido como una de las regiones del mundo de mayor importancia respecto al origen del manejo y la domesticación de numerosas plantas con fines alimenticios. Asimismo, su gastronomía es considerada Patrimonio Cultural Inmaterial de la Humanidad y los productos fermentados entran dentro de esta categoría. Los fermentos se han relacionado íntimamente como componentes importantes de la dieta mexicana, pero se han estudiado menos que las plantas yanimales comestibles. Actualmente, los alimentos fermentados tradicionales aún son diversos, pero algunos de ellos se están volviendo raros o han ido desapareciendo, y se necesitan acciones para promover su uso y conservación. La presente revisión tuvo como objetivo (1) sistematizar la información sobre la diversidad e historia cultural de las Bebidas Fermentadas Tradicionales Mexicanas (BFTM), (2) documentar su distribución espacial y (3) identificar las principales tendencias de los estudios realizados sobre ellas y los temas que se necesitan para generar una agenda de investigación que permita la conservación de BFTM que pueden estar en peligro de desaparecer yla recuperación de esas bebidas casi extintas en México. Revisamos la información y construimos una base de datos con información biocultural sobre bebidas fermentadas tradicionalmente preparadas y consumidas en México. Posteriormente, analizamos los datos a través de enfoques de red y mapeamos la información. Identificamos 16 bebidas fermentadas en su mayoría estudiadas y en general 143 especies de plantas involucradas en la producción de estas bebidas, pero tres especies de las familias *Cactaceae*, *Asparagaceae* y *Poaceae* son los sustratos centrales más comunes para las bebidas fermentadas tradicionales en México. La mayor parte de la investigación sobre microorganismos se ha dirigido a caracterizar las posibles aplicaciones biotecnológicas de los géneros Lactobacillus, Bacillus y Saccharomyces. Identificamos una brecha importante en la investigación sobre bebidas poco comunes y poca atención a los aspectos culturales, el conocimiento y las técnicas para preparar y consumir TMFB entre diferentes culturas humanas. Las bebidas fermentadas conforman paisajes alimentarios dinámicos y heterogéneos que deben considerarse como reservorios de diversidad biocultural, y deben diseñarse políticas para conservar y promover este complejo sistema de humanos, plantas y microorganismos. Este estudio aspira a contribuir a tal tarea y abrir nuevas rutas de investigación que aporten al estudio de los fermentos en el país.

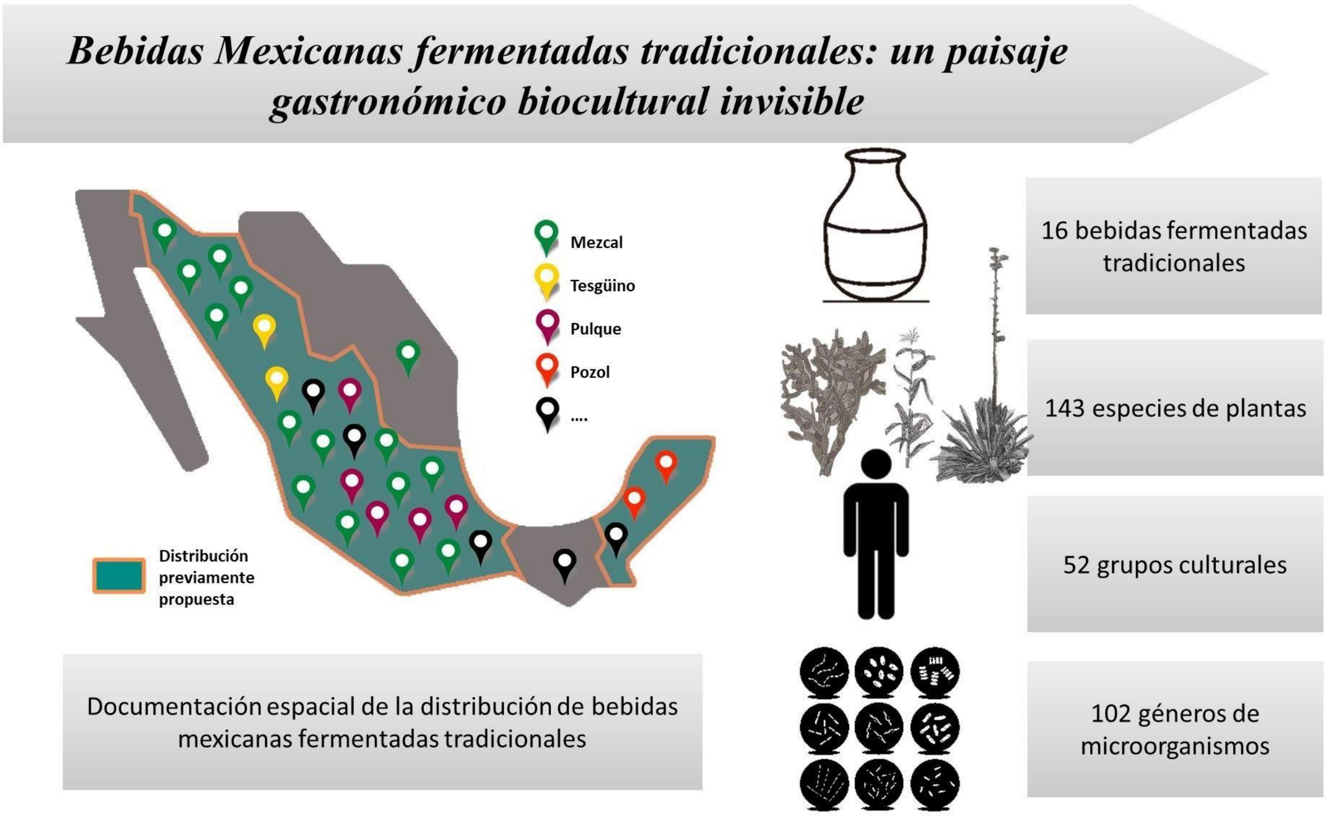
El segundo capítulo se titula “Traditional management of microorganisms in fermented beverages from cactus fruits in Mexico: an ethnobiological approach”. Es un artículo publicado en la revista de *Ethnobiology and Ethnomedicine* y se dirigió particularmente a caracterizar la elaboración de una bebida fermentada conocida como colonche. Esta es producida en distintas regiones del país a partir de distintos frutos de cactáceas. Se identificaron los sustratos vegetales con los que se preparany las técnicas de fermentación que se emplean para su producción. Además, se caracterizaron las preferencias sensoriales que son percibidas por sus productores. Las comunidades microbianas en los productos fermentados son clave en el proceso de fermentación y son seleccionados a través de diferentes procesos de manejo para lograr un producto final con características culturalmente aceptadas por las comunidades humanas. Este estudio documentó la preparación del *colonche,* la cual es principalmente producida en dos regiones de México: el Altiplano y el Valle de Tehuacán. En el presente trabajo documentamos los procesos de selección de los frutos de las especies de cactus utilizadas y las prácticas que podrían influir en la composición de la comunidad microbiana, así como las practicas que ejercen los productores para alcanzar los atributos sensoriales deseables de sus bebidas. Realizamos 53 entrevistas semiestructuradas y observaciones participativas con productores de colonche en 7 comunidades de ambas regiones con el fin de caracterizar las prácticas y procesos involucrados en la elaboración de la bebida. Se documentaron las especies de opuntia y cactáceas columnares utilizadas en la producción de colonche. Los atributos sensoriales seleccionados por los productores de colonche fueron caracterizados a partir de una tabla de clasificación y los atributos fueron contrastados visualmente a través de un análisis de componentes principales para distinguir las diferencias de esta entre los tipos de fermentación en los productores de la bebida dentro de las localidades del Altiplano. Se identificaron trece especies de cactáceas utilizadas para la producción de colonche en las dos regiones estudiadas. En el Altiplano, la fruta más utilizada es *Opuntia streptacantha* debido a que contribuye a los atributos sensoriales preferidos sobre la bebida en esta región. Encontramos que la selección de sustratos por parte de los productores depende de su preferencia y la disponibilidad de frutos de *O. streptacantha* y otras especies. Particularmente, la fermentación por la cual es producido el colonche se realiza de forma espontánea y por inoculación.En la primera la fermentación se realiza en vasijas de barro, que se considera el mejor tipo de recipiente que contribuye a las propiedades sensoriales preferidas del colonche. La segunda forma de preparación del colonche se realiza mediante la práctica de hervir el jugo de las tunas y el añadir pulque o la savia fermentada de la especie Agave como inóculo. Los atributos sensoriales máscontrastantes seleccionados entre las localidades son el contenido de alcohol y el dulzor, que puede estar de acuerdo con las prácticas utilizadas para la obtención del producto final. En la actualidad, el colonche se produce principalmente para consumo directo y, en segundo lugar, se utiliza como unbien comercializado que se vende para obtener ganancias económicas que contribuyan a la subsistencia general de los hogares. Los métodos de preparación son transmitidos por familiares cercanos, principalmente mujeres. Los productores tradicionales de colonche utilizan varias técnicas para alcanzar atributos sensoriales específicos del producto final. La producción de colonche se ha mantenido durante generaciones, pero las prácticas de fermentación se en donde se han ido incorporando distintas formas de fermentar; (1) el uso de un inóculo ya sea de pulque o de colonche guardado del año anterior, y (2) el uso de fermentación espontánea. Las diferentes prácticas documentadas reflejan los contrastes en los atributos sensoriales preferidos entre regiones. El colonche es una bebida que contribuye al orgullo regional, la identidad cultural y es apreciada por su valor gastronómico. Aquí, sostenemos que existe una clara relación del conocimiento humano en el manejo de la composición de la comunidad de microorganismos para producir esta bebida. La documentación en profundidad de la composición y dinámica de la microbiota en colonche contribuiráa la preservación de este valioso patrimonio biocultural.

El Capítulo tercero se titula “Constructing micro-landscapes: management and selection practices on microbial communities in a traditional fermented beverage”. Es un artículo publicado en la revista de *Frontiers in Ecology and Evolution*, en la sección *Conservation and Restoration Ecology*. En este capítulo se abordan cualitativamente las implicaciones que tiene el manejo de microorganismos bajo dos distintos tipos de prácticas de fermentación, los cambios en la composición, estructura y diversidad de la comunidad de microorganismos presentes en la fermentación de colonche. El colonche es una bebida fermentada tradicional producida en México mediante la fermentación de los frutos de varias especies de cactáceas. En la Región del Altiplano central mexicano, los productores usan principalmente los frutos de *Opuntia streptacantha* paraelaborar esta bebida a través de fermentaciones de tipo espontáneas e inoculadas. Distintos factores pueden cambiar la estructura de la comunidad de microorganismos a través del proceso de fermentación, sin embargo, se ha prestado poca atención al evaluar las consecuencias que tiene el manejo tradicional sobre los microorganismos. En este sentido, el presente estudio evalúa los cambios en la comunidad de microorganismos asociados a diferentes prácticas que impulsan la fermentación del colonche. Hipotetizamos que las fermentaciones continuas mostrarían una diversidad de especies de microorganismos relativamente bajas debido a la selección practicada en el inóculo y en eltratamiento de cocción. Por el contrario, las fermentaciones espontáneas expondrían una mayor diversidad debido al bajo control a las cuales están sometidas. Para probar esta hipótesis, realizamos un estudio mediante secuenciación de nueva generación de las regiones V3-V4 del gen 16S rRNA y el ITS2, para caracterizar la diversidad bacteriana y fúngica asociada a la fermentación bajo diferentes manejos. La fermentación espontánea e inoculada mostró diferencias en la riqueza de especies de microbiota, diversidad y estructura de la comunidad. Se identificó una mayor diversidad de bacterias en la fermentación espontánea, mientras que las comunidades fúngicas presentaron presentaron mayordiversidad en las fermentaciones inoculadas. Las ollas de barro donde se lleva a cabo la fermentación espontánea son reservorios de una diversidad sobresaliente de variantes de secuencias de amplicones (ASV) fúngicos y bacterianos; allí registramos la mayor diversidad de microorganismos de nuestro estudio. Como era de esperar, el inóculo mostró la menor riqueza y diversidad de todas las muestras,lo que ilustra que el conocimiento tradicional guía el manejo de una amplia gama de microorganismospara mantener y mejorar la abundancia de algunos de ellos en una comunidad. El género de levaduras más abundante en ambas prácticas de manejo es *Saccharomyces*, mientras que *Lactobacillus* y otras bacterias ácido-lácticas son las más comunes en todas las muestras de colonche, pero las técnicas de manejo influyen en su abundancia. El estudio actual proporciona un enfoque útil para evaluar las implicaciones de las prácticas de gestión sobre las comunidades microbianas en los productos fermentados y los conocimientos sobre el papel de la selección humana sobre las comunidadesmicrobianas. Estos resultados confirman el papel principal de los conocimientos tradicionales para producir bebidas fermentadas y la relevancia de los planes para su conservación.

Capítulo I

Traditional Fermented Beverages of Mexico: A Biocultural Unseen Foodscape

Cesar I. Ojeda-Linares, Gonzalo D. Álvarez-Ríos, Carmen Julia Figueredo-Urbina, Luis Alfredo Islas, Patricia Lappe-Oliveras, Gary Paul Nabhan, Ignacio Torres-García, Mariana Vallejo and Alejandro Casas.



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Review

Traditional Fermented Beverages of Mexico: A Biocultural Unseen Foodscape

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Abstract: Mexico is one of the main regions of the world where the domestication of numerous edible plant species originated. Its cuisine is considered an Intangible Cultural Heritage of Humanity and ferments are important components but have been poorly studied. Traditional fermented foods are still diverse, but some are endangered, requiring actions to promote their preservation. Our study aimed to (1) systematize information on the diversity and cultural history of traditional Mexican fermented beverages (TMFB), (2) document their spatial distribution, and (3) identify the main research trends and topics needed for their conservation and recovery. We reviewed information and constructed a database with biocultural information about TMFB prepared and consumed in Mexico, and we analyzed the information through network approaches and mapped it. We identified 16 TMFB and 143 plant species involved in their production, species of Cactaceae, Asparagaceae, and Poaceae being the most common substrates. Microbiological research has been directed to the potential biotechnological applications of *Lactobacillus*, *Bacillus,* and *Saccharomyces*. We identified a major gap of research on uncommon beverages and poor attention on the cultural and technological aspects. TMFB are dynamic and heterogenous foodscapes that are valuable biocultural reservoirs. Policies should include their promotion for conservation. The main needs of research and policies are discussed.

Keywords: ethnobiology; ethnozymology; fermentation; Mesoamerican biocultural heritage; traditional food systems

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1. Introduction

The consumption of ferments by humans probably started unintentionally since fermentation occurs in nature as a common process [1]. However, whatever its origin, the consumption of fermented foods has accompanied people since ancient times [2]. The obtaining of fermented products with desirable attributes and the conditions determining

them were eventually recognized and deliberately selected and favored [3]. Together with roasting, fermentation is perhaps one of the oldest practices and techniques used by humans to process plant and animal materials to prepare food [4]. Fermented products commonly include foods, among them beverages, but dyes, fibers, and other products involving fermentation have also been recorded since remote past times [5–7]. At some point in the human cultural history, knowledge over the fermentation process increased, hygienic practices were developed, and new techniques were adopted, outstandingly, the use of inoculums; subsequently, the manufacturing of fermented foods and beverages became the responsibility of skilled craftspersons who were mainly responsible for developing and improving the technologies for making fermented foods. Those crafters have been recognized in the literature as traditional fermentation managers [7].

Currently, a small fraction of species of organisms are predominantly used in the human diet worldwide, and this fact makes the hegemonic food systems vulnerable [8]. Fermentation plays an important role in improve the shelf life of several products, as well as to increase the diversity of food supplies and their nutritional value [9]. Therefore, the goals of diversifying food systems of the world have a key support in ferments. Most traditional ferments represent keystone products in several countries because they are expressions of interrelationships between biological and cultural diversity, and dynamic biocultural knowledge changing according to adaptive processes [9,10].

Fermented products are outputs of complex interactions of three main components, substrates, microorganisms causing fermentation, and humans who drive the process and value the final products [11,12]. Humans have observed and directed the fermentation process by choosing substrates, and selecting specific attributes of their beverages looking for pleasant-tasting, nicely textured, and long-lasting products [7,12–14]. Through time, humans have improved their techniques by experimenting with local substrates, adding others, testing variations in the general conditions of the process, and evaluating the product resulting from that process [11–16]. These biocultural practices have generated thousands of food types, including beverages, throughout human history and it is a process that continues evolving to the present day.

The fermented foods and beverages were used long before any awareness of microbiology and biochemistry [17], but now these sciences provide research tools that make it possible to identify the crucial role of microorganism assemblages in fermentation, as well as the techniques to direct fermentation according to human purposes. Microorganisms are present in substrates (plant or animal) or could be added as consortiums of microorganisms known as starter cultures. These starters may simply be small batches of previous fermentations, stored and added to new substrates to guarantee a faster and homogeneous fermentation that yields specific sensorial attributes [18–20]. Moreover, these may be microorganisms that remain in the containers where previous fermentation processes occurred, and people leave them there for new fermentation [21]. Environmental conditions are variable during fermentation, which confers variable quality and sensorial characteristics to the final product. However, traditional producers perform different practices to reduce the effect of environmental heterogeneity during the fermentation processes [7,15,22,23], while commercially fermented products are highly technified and the outcome is standardized.

Fermented beverages are among the most iconic fermented foods worldwide; these are essential components of local diets in many cultures and are mainly prepared from plant substrates [24–27]. It has been reported that through fermentation, foods may be improved, preserved, and their organoleptic properties enhanced [11]. Fermented products can have an important sociocultural role [15,24–27], consumed during holidays, ceremonies, and rituals, and linked to fruiting seasons and the harvest of agricultural products [27]. Both consumers and producers decide if the quality of a fermented product is acceptable considering their attributes and determine if it is kept or not in their diet [11–14,25–27]. Despite the importance of fermented products around the world, efforts for tracking their loss and actions to recover their production are uncommon. However, there are iconic and inspiring cases such as that in northeastern Poland, where researchers registered signs of recovering the tradition of producing juniper beers [28].

The traditional ecological knowledge involved in the preparation of fermented products appears to be at risk because of the overreliance on the massive campaigns of commercially produced beverages, which reach rural regions where the traditional products are prepared [29,30]. This fact, as well as the decline of knowledge transfer and gaps in documenting the traditional know-how of local practices to manage the microbiota, ingredients, and fermentation process have favored the marginalization and disappearance of homemade fermented products. This phenomenon contrasts with the increasing interest in the nutritional value of ferments and their economic profits in markets, especially for the trendy fermented beverages, also called functional products, for instance, kombucha [29–31].

The human diet worldwide is vulnerable since it is mostly limited to 10 to 50 plant species that provide about 95% of the world's caloric intake [32–35]. In contrast, ethnobotanists and anthropologists have documented thousands of edible species throughout the world. Only in Mexico, several studies have reported more than 2000 edible plant species, [36–40]. Among them, numerous wild species provide vegetables, fruits, nuts, tubers, and other edible products. However, little is known about the diversity of plant substrates that are employed for fermented products, their distribution, and if they are handled for specific fermentation purposes.

In 2010, the UNESCO recognized food as an intangible cultural heritage and included the Mexican gastronomy in the representative list of "Intangible Cultural Heritage of Humanity" [41,42]. However, the traditional fermented beverages are a neglected food group of the cultural heritage of the Mexican cuisine, and little is known about its conservation and biocultural status, permanence, or possible recovery. Several authors [43–46] have defined the traditional products considering the following criteria: (1) The key production steps of a traditional food product is performed in a certain national, regional, or local area, (2) the traditional food product must be authentic in its recipe, origin of raw material, and/or production process, (3) the traditional food product could have been exchanged locally for several years, available often through barter or only consumed by the family core, and (4) it is part of the gastronomic heritage. The tradition provides materials (raw substrates and tools) that allow groups to be rooted in their past and move andrebuild themselves in the present [43–46]. Therefore, it has been recognized that traditionalproducts are dynamic.

In Mexico, a broad spectrum of traditional fermented foods, including beverages, is produced from different raw materials by Indigenous and mestizo people in different regions, the processing methods and microbiota varying among regions, localities, and producers [47–50]. A previous work by Godoy and collaborators [51] reported 66 types of fermented beverages, 4 of them registered only in historical books but not consumed anymore. Most of the beverages reported by Godoy are a combination of fermented agave sap and several fruits, known as curados. Pineda [52] described over 75 types of fermented beverages, including a few distilled for preparing spirits, listing numerous herbs, fruits, roots, and stalks that were used to infuse those beverages. Bruman [53] conducted an important work in the 1930s when he visited several regions of Mexico and recorded several traditional beverages; therefore, in this study we consider his work fundamental to characterize a previous distribution of the TMFB and to compare it with the present. The previous works help to identify historically important beverages prepared with wild or cultivated plants and to determine whether the plants or the traditional knowledge and practices have become rare or lost.

Several studies have been directed to characterize the microbial communities associated with some TMFB [47–50], their possible benefits to human health [47–50], and their biotechnological and functional applications as the probiotic activity or the production of antimicrobial activity [47–50]. However, to our knowledge, none of them have been under detailed clinical trials to corroborate their benefits for human health [47–50] However, few studies have been directed to characterize the rich legacy and diversity of fermented beverages as biocultural reservoirs of diversity of organisms and the variety of practices to elaborate a culturally accepted product.

The characterization of microbial communities of Mexican fermented products has been commonly performed by culture-dependent approaches. Early classifications of products were conducted based on the physiological and biochemical criteria and microscopic inspection [51]. Nowadays, molecular markers such as 16S and ITS have been used to accurately characterize pure strains of bacteria and fungi. Nevertheless, the scope for such approaches is limited, time-consuming, and the results might dismiss the identification of uncultivable microorganisms. Culture-independent approaches have been used in other studies; for instance, denaturing gradient gel electrophoresis (DGGE) has been used to characterize the microbial communities of TMFB such as **mescal** [47,48], **pulque** [54], and **pozol** [55]. Although culture-independent techniques give insights of the composition of microbial communities, these are also time-consuming and do not provide information on rare species.

More recently, some studies have used high throughput sequencing (HTS) techniques, such as Illumina MiSeq paired-end sequencing of barcoded polymerase chain reaction (PCR) amplicons, but these studies are still scarce in TMFB. However, studies with shotgun metagenomics have recently been conducted to characterize and infer the dynamics of microbial communities of **pulque** [56,57], **atole agrio** [58], and **tuba** [59]. A few studies have been performed under a polyphasic approach but most of these studies have been used to characterize the bacterial communities, while fungal communities have not been deeply studied. The study of microbial communities in fermented products is crucial since it allows for monitoring the processes and practices and gives insights of the distinctive autochthonous peculiarities of a product. Microbial diversity is a determinant for understanding the chemistry and nutritional properties for health, yield, and quality of the plant substrates employed for fermentation [60].

This review started with the assumption that the TMFB are the outcome of the synthesis of the vast biological and cultural diversity. In particular, we expected to identify a high diversity of TMFB, which is related to the similarly high cultural diversity represented by the number of Indigenous groups that are distributed throughout the different regionsand ecosystems of Mexico. We expected that those more widely distributed and more studied groups from ethnobiological perspectives (the Nahua, Maya, Mixtec, and Zapotec in central and southern Mexico, as well as the Rarámuri, Seri, Pápago, or O'odham and the Tepehuan in northern Mexico [61]) are also those with more records of TMFB. The processes of cultural erosion have been documented in different regions, which have led to the loss of traditional cultural elements; we supposed these include TMFB. However, it is relevant to identify which ones and how much are endangered because of their decreasing availability or consumption. We, in addition, expected that those beverages based on substrates with a broader distribution and higher rooting would be the most frequent and more studied. Finally, we expected to identify a core of components of microbial communi- ties in the diverse beverages since most of the TMFB pass through a lactic and alcoholic fermentation stage. The aims of this review are therefore to: (1) Characterize the diversity of the TMFB to provide an overview of the research on fermented beverages, the cultural groups that produce them, the plant substrates used, and the microorganisms identified;
(2) visualize the spatial distribution of these beverages in the country; (3) identify their presence or absence in the foodscape and the status of conservation policies promoted by the Mexican authorities; and (4) identify the main trends of studies conducted on TMFB and the topics that are needed for a research agenda towards sustainable use of traditional ferments of Mexico. We emphasize the importance of the fermented beverages as reservoirs of biological diversity, and their relevance as Mexican biocultural heritage conferring identity to cultural groups as unique and diverse foodscapes. We, in addition, aspire to provide helpful information for designing strategies for conserving and recovering such a valuable heritage.

2. Materials and Methods

2.1. Literature Review

We conducted a search of peer-reviewed literature in Scopus, Google Scholar, Google, and the Web of Science databases to visualize the current state of research on TMFB. In addition, since numerous studies are not covered in these databases, we reviewed local journals, technical reports, books, and Ph.D. theses from regional universities of Mexico to complement the information. We also consulted references from gastronomic literature and governmental sources information. Through this search, we identified 328 peer-reviewed articles plus 197 other references related with TMFB. A search of peer-reviewed literature was performed with the following keywords: Mexican fermented beverages, traditional fermented beverages, **tepache**, **pulque**, **mescal**, **colonche**, **jobo** or **hobo**, **colonche**, **nawait**, **pozol**, **tejuino**, **tesgüino**, **piznate**, **taberna**, **cocoyol**, **tuba**, Mexican palm wine, **balché**, **xtabentún**. As these names are mainly in Spanish, we used the Boolean operators OR and AND. For example, in the Web of Science, the following search string was used: "Agave" AND "fermentation", "tradicional" AND "bebidas", "traditional" OR "ancestral" to improve the research parameters. We extended the search in local databases using keywords such as Mexican fermented beverages, bebidas fermentadas mexicanas, fermented beverages in Mexico, bebidas fermentadas en México, fermented products in Mexico, productos fermentados en México, **tepache**, **pulque, colonche**, **hobo**, Mexican wines, vinos mexicanos, **colonche**, **nawait**, **pozol**, **sidra**, **tejuino**, **tesgüino**, **taberna**, **cocoyol**, **tuba**, Mexican palm wine, and **balché**.

Most of the beverages recorded are wine-like beverages produced by the fermentation of several fruit species; however, we found numerous cases in which the producers use to add sugar cane alcohol or spirit beverages to confer specific flavors, and these beverages were not considered in our analysis. We found different names for beverages producedwith **pulque** mixed with several fruits known as *pulques curados*; in this case, we only considered the name **pulque** for all of these beverages. In a broad sense, in this review, we only considered the main substrates for fermentation and secondary substrates employed during the fermentation process.

To characterize the current state of research on TMFB, the information of the title and the abstract of each article were used as inputs in the software VOSviewer 1.6.15 [62,63]. The construction and visualization of the resulting conceptual networks were performed with the full counting method with at least three occurrences of a term, and a consideration of 60% of relevance. The layout attraction and layout repulsion parameters were scored 1 and 0, respectively, the distance between nodes represents the connectivity among concepts,and the nodes size represents the number of mentions of the concept. The clustering resolution and minimum cluster size parameters were set to 1.25 and 5, respectively.

The information from this search was systematically stored in a database using Access with the following fields: (1) Fermented product name; (2) plant substrates (both scientific and local names; (3) microorganisms (both bacteria and yeasts, and the techniques employed to identify them, e.g., culture-dependent or culture-independent); (4) ethnic groups producing and using the beverage (the dosage of consumption, related customs, and rituals; whether it is still consumed or extinct); (5) sensorial features associated to beverages (sensorial attributes reported as sweet, acid, etc.); and (6) medicinal (if it has been reported to improve human health). Searches in the databases considered studies from 1960 to August 2020. In addition, to document the conservation policies over biological resources and traditional knowledge, we searched in governmental agencies databases.

2.2. Map Construction

A map was constructed to visualize the documented distribution of fermented beverages based on the data collected in the literature; the area of the municipalities identified was considered as the documented distribution area. Another map was constructed based on the estimated distribution regions proposed by Bruman [53]. In addition, to visualizethe distribution of TMFB documented and that of the cultural groups, we considered the distribution of the Indigenous languages of Mexico reported by the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO) [64]. The map design and analysis were made with the Qgis free software [65]. Finally, a map was constructed with the overlapped data of the documented distribution and Bruman's proposal to visualize a potential area of distribution of the TMFB and the gaps that have not been documented.

2.3. *Network Analysis*

To visualize the uniqueness, diversity, and interaction of the substrates employed to produce fermented beverages, and the co-occurrence of specialist or generalist species in microbial communities, we performed an exploration through the bipartite network approach. The network's theory offers powerful tools to describe complex communities and the distribution of species specificity within them. Moreover, this approach was performed with the microorganisms identified in the literature to each traditional fermented beverage. The data from the network structure were used as descriptors of diversity and uniqueness. The analysis was performed through the Rstudio software [66] with the igraph package [67].

3. Results

3.1. *Traditional Mexican Fermented Beverages*

Based on a previous review performed by Godoy and collaborators [51], 66 types of fermented beverages were registered. Nevertheless, most of them are beverages prepared with pulque whose main substrate is the fermented sap from *Agave* plants and the addition of fruits of native and introduced plant species. By the current review, we identified 16 names for traditional fermented beverages produced from several substrates such as seeds, stems, fruits, tree barks, fruit pulps, and sap. Stems are the dominant substrates used for preparing traditional fermented beverages. We identified 140 plant species used as main substrates for fermentation or as promoters of fermentation.

Through the peer-reviewed literature, we identified 10 traditional fermented beverages and we extended the number of studies based on the information from theses and the local literature, from which we identified 6 additional beverages; therefore, we documented a total of 16 fermented beverages. The most studied beverages are **mescal**, **pulque**, **tejuino**, **pozol**, **chorote**, **colonche**, **saká**, **sendechó**, **balché**, **atole agrio**, **pox**, **sambudia**, **tesgüino**, **tepache**, **tuba,** and **taberna** (Table 1).

Since we did not find recent studies on other beverages, we cannot confirm what is their actual status of production and distribution. Clearly, further field studies should be directed to document what is currently happening with these beverages. It can be visualized that the current research tendency is markedly directed towards the beverages grouped into the category of *Agave* spirits or *Agave* distillates referred to in this study as **mescal**, compared with the rest of the traditional fermented beverages in peer-reviewed literature.

The current state of research in peer-reviewed articles on TMFB can be visualized in the network of Figure 1, which displays nine conceptual clusters that highlight the main topics related to the beverages. Cluster (1) (in red) is related to the application, evaluation, and sensory properties of the fermented products. This cluster resembles the classical biotechnological approach from the early 1990s, most of the research being directed to improve the sensory properties of **mescal.** It also includes new trends related to the application of defined starter cultures. Cluster (2) (in green) is the **mescal** cluster, in which *Agave potatorum* appears as the most studied species, and *Saccharomyces cerevisiae* as the most commonly characterized microorganism. This cluster highlights the economic importance of **mescal** production, and the interest in improving the fermentation profile using several *S. cerevisiae* strains. Cluster (3), the yeast cluster (in blue), emphasizes the use of non-*Saccharomyces* yeast species to improve the aroma profile and optimize the ethanol production in **mescal.** Cluster (4) is the pathogens cluster (in olive) and refers to the effects of pathogens such as *Scyphophorus acupunctatus*, which mainly affect the *Agave* groups, decreasing the production of beverages related to these plants. Cluster (5) is the *Agave* *salmiana* cluster (in purple), which is mainly related to the influence of environmental factors in the development of plants and the fermentation process.

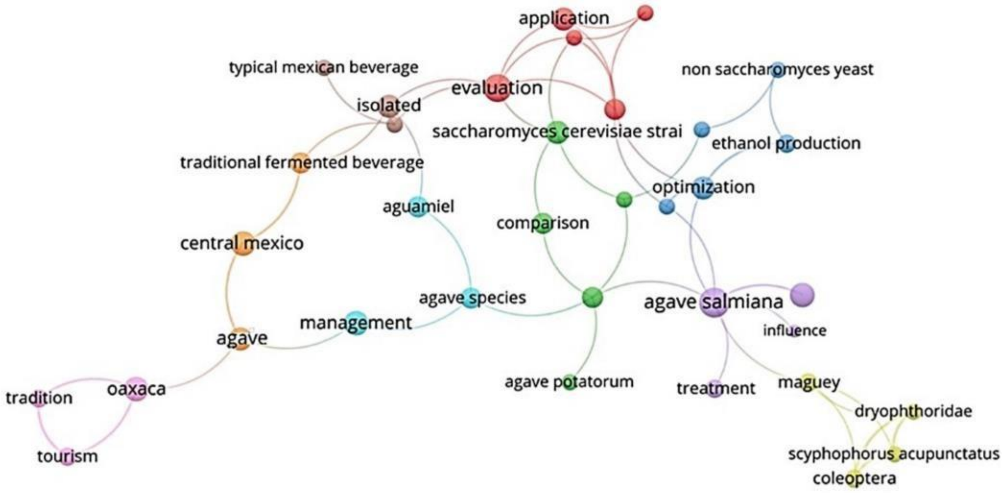

Figure 1. Clusters representing different research topics reported in the literature. The red cluster • is related to biotechnological applications in traditional fermented beverages; the green cluster • represents studies related to the mescal production; the blue cluster • are those on the application of yeasts through the production of traditional fermented beverages; the olive cluster • includes studies on pathogens affecting the development of *Agave*; the purple cluster • comprises the research on environmental factors influencing the fermentation process; the light blue cluster • are studies on management practices of *Agave* and sap extraction; the orange cluster • indicates the reports on the presence of traditional fermented beverages in central Mexico, mainly **pulque** and **mescal**; the brown cluster • shows the research that has been directed to maize beverages and the possible probiotic features associated with this microbiota; the pink cluster• shows the importance of cultural groups of related to production of fermented beverages, but it is only related with mescal production.

The following clusters are related to the most traditional beverages and human groups related to them: Cluster (6), the management cluster (in light blue), groups the management practices on *Agave* species, mainly those involved in the production of **pulque** and the implications of management of agaves for sap extraction. Cluster (7), the one of traditional fermented beverages (in orange), features the less common traditional fermented beverages prepared in central Mexico, those with *Agave* species such as **pulque** or **mescal** that occur mainly in central Mexico. Cluster (8), the maize group (in brown), mainly accounts for research directed to isolate and characterize the bacteria and yeasts associated to possible probiotic attributes in **tejuino** and **pozol**. Cluster (9), the cultural cluster (in light purple), groups studies related to traditions and tourism, mainly in the state of Oaxaca. It can be highlighted that this cluster is also related to **mescal** production.

Table 1. Main traditional Mexican fermented beverages. Main substrates for fermentation, microorganisms described, and cultural groups associated to its production.

Beverages	Main Substrate	Main Microorganisms Recorded in the Literature	Cultural Groups Associated	Literature
Pozol	*Zea mays* (grains)	**Bacteria**: *Aerobacter, Acetobacter, Achromobacter, Agrobacterium, Alcaligenes, Bacillus, Bifidobacterium, Clostridium, Enterobacter, Enterococcus, Escherichia, Exiguabacterium, Klebsiella, Kosakonia Lactobacillus, Lactococcus, Leuconostoc, Paracolobactrum, Pediococcus, Pseudomonas, Propionibacterium, Streptococcus, Weissella.* **Yeasts**: *Candida, Cyberlindera, Debaryomyces, Kluyveromyces, Galactomyces, Meyerozyma, Pichia, Rhodotorula*, *Trichosporon*. **Fungi**: *Cladosporium, Monilia, Mucor, Phoma, Penicillium.*	Chol, Chontal, Lacandon, Mam, Maya, Tojolabal, Tzeltal, Tzotzil, Zapotec, Zoque, Mestizo	[52–55,61,68–70] [71–79]
Atole agrio	*Zea mays* (grains)	**Bacteria**: *Acetobacter, Aerococcus, Bacillus, Enterococcus, Clostridium, Lactobacillus, Lactococcus, Leuconostoc, Pediococcus, Streptococcus,* Weissella. **Yeasts:** *Candida, Cryptococcus*, *Clavispora*, *Debaryomyces*, *Hanseniaspor, Pichia Saccharomycesa.* **Fungi:** *Aspergillus, Fusarium, Penicillium.*	Maya, Mazatec, Nahua, Purepecha, Totonac, Tzeltal, Tzotzil, Wixarika, Mestizo	[58,72,73,80–83]
Saká	*Zea mays* (grains)	ND	Maya, Tzotzil, Tzeltal	[84]
Tejuino	*Zea mays* (grains)	**Bacteria**: *Acetobacter, Bacillus, Brochothrix, Chyseobacterium*, *Kurthia, Lactobacillus, Leuconostoc, Pantoea, Pseudomoonas, Strotococcus, Weissella*. **Yeasts**: *Candida, Galactomyces, Lachancea, Meyerozyma, Saccharomyces, Wickehamomyces.***Fungi** .*Aspergillus, Penicillium*	Mestizo	[85,86]
Tesgüino	*Zea mays* (grains)	**Bacteria**: *Bacillus, Lactobacillus, Bacillus, Leuconostoc, Pediococcus, Streptococcus*. **Yeasts**: *Brettanomyces, Candida, Clavispora, Cryptococcus, Kluyveromyces, Lachancea, Metschnikowia, Meyerozyma, Pichia, Saccharomyces, Wicherhamomyces*. **Fungi**: *Aspergillus, Penicillium*.	Guajiro, Pame, Pima, Tarahumara, Tepehuan, Tubar, Wixarika, Yaqui, Zapotec	[46–49,87–92]
Pulque	*Agave* spp. (sap)	**Bacteria**: *Acetobacter, Acetobacterium, Acinetobacter, Acrobacter, Adlercreutzia, Ardescatena, Bacillus, Commensalibacter, Citrobacter, Cellulomonas, Cellulosimicrobium, Chelativorum, Chryseobacterium, Chryseomonas, Clostridium, Comensalbacter, Corynebacterium, Devosia*, *Dysgonomonas*, *Enterobacter, Erwinia, Escherichia, Euzebia, Flavobacterium, Fructobacillus, Gluconobacter, Hafnia, Halomicronema, Kluyvera, Klebsiella, Kokuria, Komagataeibacter, Lactobacillus, Lactococcus, Luteomicrobium, Leuconostoc, Marivitia, Macrococcus, Mesorhizobium, Micrococcus, Microbacterium, Micrococcus, Novosphingobium, Providencia, Pediococcus, Pseudomonas, Rhodobacter, Rhodovulum, Ruminococcus, Sacrcina, Salinibacterim*. *Sarcandra, Serratia, Sphaerotilus, Sphingomonas, Sphingopyxis, Streptococcus, Streptomyces, Sulfuropirillum*, *Synechococcus*, *Tanticharoenia*, *Trochococcus, Weissella, Zymomonas*. **Yeasts**: *Bullera, Candida, Clavispora, Cryptococcus, Cystofilobasidium, Debaryomyces, Dekkera, Galactomyces, Hanseniaspora, Kazachstania, Kluyveromyces, Lipomyces, Meyerozyma, Pichia, Rhodotorula, Saccharomyces, Schwanniomyces. Torulaspora*, *Westerdykella, Wickerhamomyces, Zygosaccharomyces*. **Fungi**: *Aureobasidium*. *Aspergillus*, *Cladosporium*. *Penicillium*, *Rhizopus.*	Hñähñu, Ixcatec, Mazahua, Mixtec, Nahua, Ngiwa, Purhepecha, Triqui, Zapotec, Mestizo	[23,45–48,93–97]

Table 1. *Cont.*

Beverages	Main Substrate	Main Microorganisms Recorded in the Literature	Cultural Groups Associated	Literature
Tuba	*Cocos nucifera* (sap)	**Bacteria**: *Bacillus*, *Cronobacter*, *Enterococcus*, *Erwinia, Fructobacillus*, *Gluconacetobacter*, *Klebsiella, Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Micrococcus*, *Serratia, Sphingomonas*, *Vibrio*, *Zymomonas.* **Yeasts**: *Candida*, *Cryptococcus*, *Hanseniaspora, Saccharomyces.*	Mestizo	[96,98–115]
Taberna	*Acrocomia acuelata* (sap)	**Bacteria**: *Aerobacter*, *Acetobacter*, *Bacillus, Brevundimonas, Citrobacter, Enterobacter, Enterococcus, Fructobacillus, Gluconobacter, Klebsiella*, *Kluyvera*, *Lactobacillus*, *Lactococcus, Pantoea*, *Sphingomonas, Zymomonas.* ***Yeasts***: *Candida*, *Hanseniapora, Issatchenkia, Kazachstania. Meyerozyma*, *Pichia. Rhodotorula*, *Saccharomyces, Schizosaccharomyces*	Zapotec, Mestizo	[98–100]
Tepache	*Ananas comosus* (fruit)	***Bacteria***: *Acetobacter, Acinetobacter, Bacillus*, *Escherichia, Enterobacter, Enterococcus, Gluconobacter, Klebsiella, Lactobacillus, Lactococcus, Leuconostoc, Micrococcus, Pediococcusa, Weissella.* ***Yeasts****: Candida, Cryptococcus, Hanseniaspora, Meyerozyma, Pichia, Rhodotorula, Saccharomyces.* **Fungi**: *Penicillium.*	Mestizo	[49,50,116–118]
Colonche	*Opuntia* spp. (fruits), *Pacchycerus, Stenocereus*	**Bacteria**: *Enterococcus*, *Lactobacillus*, *Leuconoctoc*, *Pediococcus, Weissella.* **Yeasts**: *Candida*, *Hanseniaspora*, *Pichia, Saccharomyces.*	Chichimecan groups, Pame, Zapotec, Mestizo	[22,50,52,119]
Mescal	*Agave* spp.	**Bacteria**: *Acetobacter*, *Acinetobacter, Acetobacterium*, *Bacillus*, *Citrobacter*, Enterobacter, Erwinia, Chryseobacterium, *Gluconobacter*, *Kluyvera*, *Kokuria*, *Komagataeibacter*, *Lactobacillus*, *Lactococcus*, *Leuconostoc*, *Microbacterium*, *Providencia*, *Oenococcus*, *Pediococcus*, *Pseudomonas Serratia*, *Weissella*, *Zymomonas*. **Yeasts**: *Candida*, *Citeromyces*, *Clavispora*, *Cryptococcus*, *Debaryomyces*, *Dekkera, Diutinia*, *Hanseniaspora*, *Issatchenkia*, *Kazachstania*, *Kluyveromyces, Meyerozyma, Millerozyma*, *Naganishia, Ogataea, Pichia*, *Pseudozyma*, *Rhodosporidiobolus, Rhodotorula*, *Saccharomyces*, *Saturnispora*, *Schizosaccharomyces Sporidiobolus*, *Torulaspora*, *Trichosporon*, *Wickerhamomyces, Yamadazyma*, *Zygosaccharomyces.*	Cahiti, Guasave, Ixcatec, Pima, Tepehuan, Warohiro, Wixarika, Mestizo	[116,120–126]
Chorote	*Zea mayz (grains)* *Theobroma cacao* rosted beans),	*Fructobacillus*, *Lactobacillus*, *Leuconostoc*, *Gluconacetobacter*, *Sphingomonas*, *Vibrio,*	Maya, Mestizo	[127]
Balché	*Lonchocarpus* spp. *(bark and flowers)* and honeybee	**Yeasts**: *Saccharomyces.*	Lacandon, Maya	[84,128–133]
Pox	*Saccharum officinarum* and *Zea mays (stems)*	ND	Chol, Tzeltal, Tzotzil Mestizo	[53]

Table 1. *Cont.*

Beverages	Main Substrate	Main Microorganisms Recorded in the Literature	Cultural Groups Associated	Literature
Sambudia	*Ananas comosus* (fruit)	ND	Mazahua, Mestizo	[134–136]
Sendechó	*Zea mays (grains)* and *Capsicum* sp.	**Bacteria**: *Acetobacter, Bacillus, Enterococcus, Klebsiella, Kocuria, Lactobacillus, Leuconostoc, Micrococcus, Pediococcus, Pseudomionas, Staphylococcus, Zymomonas.* **Yeasts**: *Candida, Clavispora, Cryptococcus, Galactomyces, Kluyveromyces, Rhodotorula, Saccharomyces*, *Torulaspora, Wickerhamomyces, Zygosaccharomyces.* **Fungi**: *Aureobasidium, Cladosporium, Epicoccum, Fusarium, Paecilomyces, Penicillum, Phima, Sclerotium, Verticillium.*	Mazahua, Hñähñu	[48–50,137–141]

ND: No data recorded.

The network shows that most of the current research is directed to study the **mescal** production process and its optimization. This is not surprising because of the national and international rising market boom of **mescal**. However, it is lower than research on tequila, which is the fourth largest export product of Mexico [142]. After **mescal**, **pulque** is the most studied beverage, particularly biotechnological and management aspects involved in its production.

3.2. Current State of the Conceptual Overview

The main microorganism referred to in the studies is *S. cerevisiae*, which is a common species in fermented products around the world and it is frequently found in alcoholic beverages. Surprisingly, it is possible to see in the network that the non-*Saccharomyces* species form a node; this is a trend around several industrialized beverages, such as beer [70], wine [143], and recently in cocoa fermentation [144], which looks for flavors and aromas in the final products. Research has been directed to characterize bacteria in the traditional fermented beverages, mainly because most of these beverages pass through a lactic fermentation stage, but perhaps the most common purpose is the isolation and evaluation of these bacteria to improve human health [145].

Two major trends can be identified in the current research on traditional fermented beverages in Mexico. The first one includes biotechnological approaches, which could be visualized in the first three clusters referred to above, which is related to the world- wide interest of the dairy industry to promote products with probiotic and prebiotic compounds [146]. This topic has been constitutively addressed in numerous research centers for several beverages around the world [147]. In the markets, there is an increasing demand for functional dairy products and healthy food [148,149] that pushes this major trend, which is reinforced by the search for options to improve nutrition in developing countries by using biotechnology [87,150]. In Mexico, this trend is clear in fermented beverages such as **pozol**, **pulque**, **tepache** and **tejuino**, whose microbiota and potential benefits to health have been majorly characterized.

The second research trend is related to the *Agave* beverages such as **pulque** and **mescal,** but also beverages such as **pozol**, which entails biotechnological approaches and the traditional management of sources of substrates, particularly *Agave* species. The rising market of **mescal** appears to be leading this trend, while in the case of **pulque**, the possible food functionalities appear to be the main drivers of the current research programs. It is possible to see the great cultural node related to **mescal** production, but few studies focused on the cultural groups in other beverages.

There is a huge gap in the research agendas on traditional fermented beverages. It is notorious the major interest that *Agave* products have but almost null on the rest of the traditional fermented beverages. As mentioned, there is high interest in biotechnological research programs specially to explore the central region of Mexico, which could be seen in Figure 4A. The remaining beverages are not only marginalized in markets, but also in the scientific agendas. Greater efforts to maintain them should be performed.

3.3. Plant Diversity Used in Mexican Traditional Fermented Beverages

We identified 143 plant species used as main and secondary substrates for fermentation, as promoters of the fermentations process, and as additives to improve the shelf life or flavor (see Table S1). The network analysis reported a low connectance, a low number of links between the species and beverages analyzed, which elucidates the high specialization of ingredients, preparation, and assemblages of the beverages as can be seen in Figure 2, in which the clusters are relatively distant from each other (see also Table 2). This pattern is corroborated with the low niche overlap and the mean of shared partners in the network. The latter value also explains the low number of generalist species involved in the network; species such as *Z. mays (Z)*, *A. salmiana (A)*, *S. officinarum (S)*, and *Cinnamomum verum (C)* can be seen involved in the production of different fermented beverages. *S. officinarum* is a species frequently employed to strengthen fermentation as it is used as an external supply of sugars, commonly added as processed brown sugar. *C. verum* is used to add different flavors to the final product but not during the fermentation process. Cinnamon has been recorded to have antimicrobial and pathogens inhibitors properties, but it has not been reported on its use to avoid spoilage. Sugarcane and cinnamon are non-native species from Mexico but are strongly integrated into the traditional fermented beverages production as enhancers or additives.

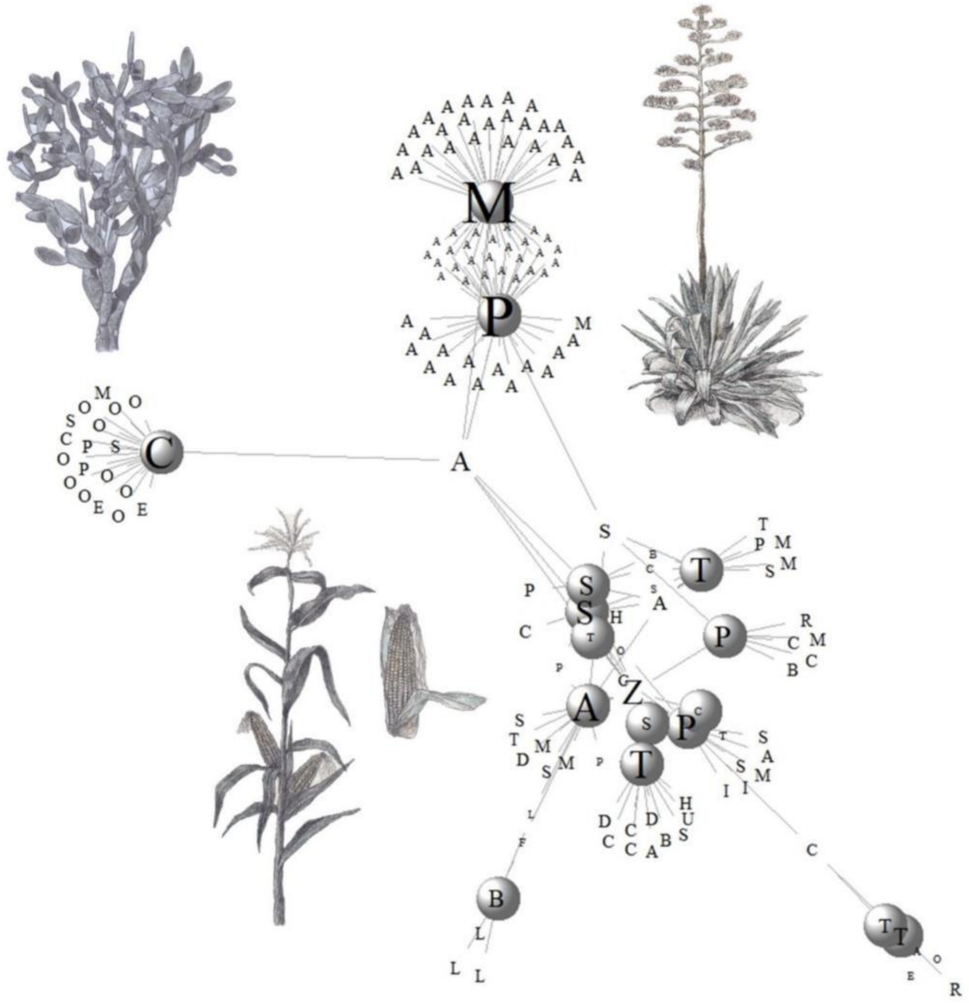

Figure 2. Network of substrates. Capital letters in the grey circles represent the TMFB, the sizeof circles and letters are related to the number of substrates employed; the letters without circles represent the species employed in fermentation, their size represents the number of uses in different fermented beverages. The M and P clusters are related to the substrates used for preparing **mescal** and **pulque**, respectively; the A represents the *Agave* species employed. The A in the middle of **pulque** and **mescal** cluster represents shared species, while in the external position represents exclusive agave species. The *C* circle is the **colonche** production, it is prepared with several cacti fruits, and shares *A. salmiana* for its production as other beverages in which the A is in the center of the network. The centered cluster is related to maize produced beverages (**pozol**, **tesgüino**, **tejuino**, **atole**, **chorote**, **saká**) in which *Z. mays* (Z in the middle) is the core substrate for these fermented beverages. The B cluster is the **balché** group, in which L letters refer to *Lonchocarpus* spp.; the T cluster is related to beverages prepared mainly by the fermentation of palm sap such as **taberna** and **tuba**. Species and beverages are listed in the Table S1. Illustration credits to Rosa Jeannine Xochicale Solís.

Table 2. Network values for plant substrates and microorganisms.

Network	Connectance	Links per Species	Niche Overlap	Mean of Shared Partners
Plant substrates	0.085	1.29	0.20	0.31
Microorganisms	0.23	1.75	0.99	7.21

The network of substrates of the traditional fermented beverages of Mexico is diverse ($S = 5.21$), with a minimal connectance, which indicates the uniqueness of most of the beverages with a high specificity in the substrates. The documentation and protection of those unique substrates should be attended to maintain and guarantee their production. The network allows for visualizing that maize is the most generalist substrate, which is not strange since maize is a keystone of the Mexican food systems and cultures and is prepared in great diverse ways.

3.3.1. Cluster of Maize Beverages

Eight TMFB involve the use of maize as a main or secondary substrate, most of them are prepared with maize grains, including: **atole agrio**, **saká**, **tejuino**, **tesgüino**, **sendechó**, **chorote**, and **pozol**. **Pox** was usually prepared with maize stems as the main substrate, but sugarcane stem is more commonly used now. For processing most of these products, people employ specific races of maize; we identified 21 races used to produce them, and the beverages receive different names according to the maize race and locality where they are produced. Beverages produced with maize have a deeply and strong relationship with ethnic groups. Through this review, we identified that maize beverages are the most consumed by 21 cultural groups of Mexico.

Tesgüino is produced and consumed mainly by the Rarámuri or Tarahumara people and other cultural groups such as the Yaqui and the Wixarika, who live in northern Mexico [46–49,87–90]. This beverage is commonly mentioned as the Mexican beer or maizebeer, and locally named batári by the Tarahumara. It is consumed for several cultural purposes related to celebrations such as weddings, funerals, rituals associated to practices of the agricultural cycle, baptisms, and for maintaining the cohesion of the communitiesin the celebrations called tesgüinadas [90]. It is a beverage mainly elaborated by women by fermenting sprouted maize kernels. About five days after germination, kernels are grounded and boiled for approximately 12 h, then cooled, and the mass obtained is placedin a container known as tesgüinera where fermentation takes place. It is a spontaneous fermentation where producers commonly add leaves and other parts of local weeds and trees such as *Stevia serrata*, *Chimaphila maculata*, *Datura meteloides*, *Hamaemelum nobile,* and *Cojoba arborea,* all of them identified with local names [90–92]. *Usnea dillenius*, a lichen, is used as a catalyst [90].

It is commonly assumed that **tejuino** and **tesgüino** are the same beverage since the fermentation core substrate in both cases is the grounded kernels of maize (a dough); however, the process, the plant species, and the varieties added, locations, and the cultural groups are different. **Tejuino** is a TMFB prepared with the dough of one variety of maize and the addition of brown sugar. It is mostly consumed in the states of Colima and Jalisco by mestizo people, and non-special containers are used for fermentation. The **atole agrio** is a similar beverage. It is the fermentation of maize dough, and no sugar is added. It has been recorded in southern Mexico and its consumption involves the use of different localraces of maize among the localities.

Pozol and **saká,** are non-alcoholic fermented beverages from the Mayan region, prepared with dry corn kernels, boiled with calcareous stones and then grinded into a dough. This is a process of nixtamalization that confers a particular consistency and flavor to the dough and adds nutrients such as calcium oxide and others that become bioavail- able [54,81,151]. This maize dough can be prepared with several maize races available inthe region. For both beverages, the process is clearly similar, but **pozol** is more common among the mestizo communities and **saká** is associated to Indigenous communities in religious contexts. For its production, maize dough is stored into small balls in banana leaves until fermentation, a process that varies depending on the environmental conditions and the producers' preferences. The dough balls are dissolved in water and consumed as a daily beverage [54,81–83,91,92,151]. In different locations, **pozol** dough can be mixed with batata, toasted cocoa, coconut, cinnamon, or vanilla [72–76]. These beverages are consid- ered a source of nutrients and an essential food in southern Mexico, where its consumption is associated with traditional ceremonies, or consumed as a daily drink. It is also consumed as remedy for gastrointestinal illnesses in some localities [54,76–79].

Sendechó is a beverage that can be prepared with several maize races (five reported), depending on the producers' preferences, so its final color might vary from light red to purple, light yellow, white, and black. Through the germinating grains step, *Buddleja americana* is mixed with the grains [48,49]. **Pulque**, called ixquini in the region, is added as a starter inoculum [137,138]. The production process is similar to those maize beverages mentioned above; sprouted maize grains are ground, in this step chili peppers could be added [138], and then a maize dough is boiled with water, it is filtered with a cloth, and then spilled in a clay pot where *Agave* sap or fermented sap can be added as a starter of fermentation. It is produced in areas close to Mexico City and is still consumed by the Mazahua, Otomi, and mestizo groups for several cultural purposes.

3.3.2. Cluster of Agave Beverages

The cluster of *Agave* beverages is a highly diverse group, with 68 agave species involved in the fermentation of **pulque** and **mescal** as the main substrate to produce both beverages. The fermented sap of *A. salmiana* is the most frequently employed to produce **pulque** and it is also added as an inoculum to other beverages. Although *Agave* is a diverse group, we recorded low connectivity among its components, which suggests unique fermented products. Since species and varieties of *Agave* are not explicitly recorded in some studies, we might be underestimating their distinctiveness; there are several local names for the local varieties, suggesting high variation, but unfortunately, their taxonomic identity has been insufficiently studied and indicated.

Mescal appears to be the predominant beverage of *Agave* throughout the Mexican territory. It is in fact the beverage that employs a major number of species to get a final product, most of them are locally distributed and different species are often mixed to produce a unique sensorial profile. We consider **mescal** as a TMFB because most of the species employed for its production are endemic to Mexico, and most of them wild but some have gone through a domestication process or are under different levels of domestication by people of this country. Moreover, because these products are locally and/or regionally produced, their production is mostly unique for each producer, are part of the local gastronomic heritage, and include local and foreign technologies as mentioned before [45–48]. This group is highly variable in the production process among regions and producers, using different substrates, fermentative spaces, types of containers, and fermentation techniques. In fact, local names for mescal spirits are diverse and depend mostly on the region and substrate employed. The basic fermentative substrates are the cooked *Agave* stems and foliar bases whose products are then distilled; however, the species used are numerous and variable among the regions.

As mentioned, we did not consider other plant or animal products that are often mixed with pulque consumption which are generally called pulques curados [93–95]. We did not consider them because the main substrate is the fermented agave sap and fruits are added after **pulque** is produced. Moreover, we did not consider the species that are used as tools, such as *Lagenaria siceraria*, to store or transport the sap of *Agave* species. However, the number of *Agave* species employed as main substrates for **pulque** production (42 species) is high. **Pulque** results from the fermentation of *Agave* sap, and it has been recorded as spontaneous fermentation [91,92], but also as the product of using inoculums, which have been characterized in different regions [23,93–96]. **Pulque** preparation starts with the collection of the agave sap called aguamiel directly from the agave stem, which is mostly performed under non-sterile conditions [95,96]. The fermentation process varies depending on the agave species, the quality of the sap, the region, and other factors. There is not one single type of **pulque** because of the plethora of practices, species, and conditions for its production. These practices might change the fermentation process in time, the assemblages of yeasts and bacteria, and the final sensorial attributes.

Pulque has been used historically for festivities, ceremonies, agricultural rituals, births, and funerals [93]. There is a specific regulatory system for **pulque** in Mexican law (NMX-V-022.1972), which defines quality standards and sensorial attributes. In addition to the health benefits of **pulque** or its biotechnological applications, the diversity of plants employed and the practices performed reflect a historical know-how developed by humans in interaction with their local environments. However, this production system has been marginalized.

3.3.3. Cluster of Cacti Beverages

Colonche is a traditional fermented beverage that can be prepared with fruits of at least 17 cacti species. **Colonche** is the common name of this beverage in the region of the Altiplano central region of Mexico, where it is mainly prepared with several *Opuntia* species,although the most common and preferred by the producers and consumers is that prepared with *O. streptacantha* [22,50]. **Nawait** is another common name for a fermented beverage mainly produced by the fermentation of *Carnegiea gigantea* fruits, whose distribution covers the Sonoran Desert in northern Mexico and the southwestern U.S.A. [52]. In this region, a **colonche**-like beverage is also prepared with *Pachycereus pringlei*. In the Tehuacán-Cuicatlán Valley in south-central Mexico, **colonche** is known as nochoctli or pulque rojo. There, the fruits of several cacti are employed to produce this fermented beverage, the most common are those of *Pachycereus weberi*, *Escontria chiotilla*, and *Stenocereus* spp. This beverage is produced in different seasons depending on the availability of the substrates. For instance, in south-central Mexico, colonche is produced in April–May and in August–September, when fruits of the different species of columnar cacti and *Opuntia* used to produce it are available. The production and fermentations practices of **colonche** are variable in the different regions [22]. In most regions, fermentation occurs spontaneously; nonetheless, inoculums are employed by some producers by the addition of pulque from *A. salmiana* or by using inoculums from previous fermentations of cacti fruits. Most of the fermentations occur in clay pots continually used and that have been maintained by several generations of the managers [22].

3.3.4. Cluster of Palm Beverages

The beverages **tuba** and **taberna** form the palm cluster. These are prepared by the fermentation of the sap extracted from different palm trees, similarly as it is carried out with other palm wines consumed around the world, such as legmi in Africa, or kallu in southern India, as well as several Asian palm wines [98,99]. The main differences of these beverages are the palm species and the palm parts from which sap is obtained [99,100]. These beverages were adopted in Mexico by the Philippine influence during the Spanish colonial period and are currently produced in the Pacific coastal zones of Mexico. The species used for producing **taberna** is *Acrocomia aculeata* known as coyol, and it is produced in localities of the southern state of Chiapas [100,139–141,152–155]. The production occurs by the deliberate cut of the shoot apical meristem of the palm tree, then by making a cavity where sap is accumulated and fermented. The cavity is covered to avoid contamination by insects and then the sap is collected and consumed fresh. Sap for preparing **tuba** is obtained from the inflorescences of *Cocos nucifera*, which is collected and then stored in plastic containers, although the iconic containers are those manufactured with *L. siceraria* fruits, which are called bules [98–100,139–141,152–155].

3.3.5. Balché Cluster Beverages

Balché is an exceptionally important TMFB since it is the sacred drink for the Mayan, consumed in several ceremonies. It is the result of the fermentation of bark from several *Lonchocarpus* species, among them *L. punctatus* or *L. violaceus*, and *L. longistylus*, which is mixed with honey (either from *Apis mellifera* or melliponini bees). It has a particular pink color and sweet taste, and has been consumed since pre-Hispanic times [84,128–132]. To produce this beverage, some producers boil the bark of the tree to remove the compounds that confer a bitter flavor, thus the bark releases its characteristic color and fragrance. Then, it is dried to later be boiled with virgin water, which is collected from cenotes or rivers. After that, the bark, honey, and water are mixed and fermented spontaneously in a hole made inside a tree; later, the hole is sealed with banana or palm leaves for two or three days. Hitherto, *S. cerevisiae* has been the only microorganism recorded in the fermentation of this beverage [133], but more studies are clearly needed.

3.3.6. The Cluster of Tepache and Sambudia

Tepache can be prepared with at least 10 plant species as a substrate. Nowadays, in central Mexico the most common substrate is pineapple (*Ananas comosus*), but its etymology in the Náhuatl language derives from tepitl, a beverage made with maize in the past and in few localities [49,50], which suggests that this beverage is a derivation from an ancient maize beverage. In western Mexico, **tepache** is also produced by the fermentation of other fruits that belong to the Bromeliaceae family, such as *Bromelia karatas*, known as tumbiriche or timbiriche. It can also be prepared with fruits of plants introduced into Mexico such as apple, orange, and guava [117,118]. In the case of **tepache** prepared with pineapple, the process starts by peeling the infrutescences and adding the rind into a wooden container known as tepacheras, then brown sugar is added. It is a spontaneous fermentation where the microbiota is mainly associated with the sorosis epidermis [49,50]. Production of **tepache** with other fruits can be fermented in plastic containers; this beverage is commonly homemade, and its quality varies from kitchen to kitchen.

Sambudia is a beverage prepared with several substrates, including maize, rice, and barley. **Sambudia** is the name used for different beverages produced in the state of Mexico; a first way to produce it is using pineapple peel as a substrate [50,134–136] through a process similar to that of **tepache**. A second way to prepare it is with ground grains of rice, or barley; in this case, cinnamon, cloves, pepper, roasted and ground maize leaves, and pulque are added in a container; brown sugar is added to sweeten the mixed elements and the mixture is fermented for at least one day [136]. Moreover, it can be prepared with the fermentation of *B. karatas* fruits by adding pineapple peel, maize leaf, and ground maize. Fermentation occurs by inoculating the remnants of past fermentations in the containers, which are clay pots called sambudieras [134].

3.4. Traditional Fermented Beverages as Dynamic Systems: The Addition of New Substrates

The historical records indicate that practices and techniques for manufacturing fermented foods evolved independently in every hemisphere and were developed based on the resources available in the local environments [12]. In Mexico, the fermented beverages, practices, and techniques are applied on the three main groups of substrates referred to above. However, the inclusion of foreign species or technologies to diversify the diet are not an exception in the Mexican cuisine. Therefore, rather than cultural erosion, the contact with new species, ingredients, and techniques of the Old World appears to have enriched the Mexican fermented beverages. These historical processes support a diversification hypothesis [101].

As humans migrated from region to region, food cultures and production practices moved as well [12,101–105]. Although the most common plants used as main substrates to produce fermented beverages are maize, agaves, and columnar cacti, the inclusion of new species replaced some substrates. A clear example is the traditional fermented beverage **pox** prepared with the stems of *Z. mays* nowadays, mainly prepared with *S. officinarum* stems [53], but also the several beverages with added brown sugar from this crop originating in Southeast Asia [106]. *C. verum*, also originated in Asia [107–109], is commonly used as an additive to flavor several Mexican beverages.

The fermentation of numerous palms sap is common in countries of Asia andAfrica [96,98–111] and, in Mexico, **taberna** and **tuba** are examples of the adoption of new technologies and instruments, including distillers for the Philippine coconut spirits distillation technique [112–114]. Nowadays, there is a debate about possible pre-Columbian distillation, but the fact is that the Philippine distillation technique is commonly used in several localities for producing **mescal** and other beverages [115].

3.5. Traditional Knowledge and Microbial Communities in Fermented Beverages: How Do Traditional Fermenters Promote Microbial Reservoirs and Microbial Diversity

The most common practice to promote fermentation worldwide is the inoculation of a substrate with starter cultures. For instance, in Korea, soy sauce is prepared using meju (solely fermented soybeans), whereas in Japan and China it is prepared using koji (a fermented mixture of soybeans, wheat flour, and wheat) [156]. Similar examples exist around the world and, recently, the use and characterization of starter cultures has been a main trend of research that could be used to improve fermentations and prevent the possible risk of spoilage [157–159]. This is, for instance, the case of traditional and industrial production of wines [160–164]. However, there are still few studies identifying and characterizing traditional starter cultures for traditional products in Mexico.

Through this review, we identified names such as tibicos, castaña, xinaiste, jinaiste, zinaiste, el pie, el pie de pulque, asiento, ixquini, semilla, xaxtle, and nancle among the most frequent names that fermenters give to those mixed starter cultures for traditional fermented beverages. The study and characterization of these microbial communities have only been scarcely covered in studies of beverages such as **mescal** [97,165], **pulque** [61,166,167], and recently in **atole agrio** [21]. This technique has been used for years and the methods to prepare them should be considered in further studies.

A commonly accepted assumption in traditional fermented products is that spontaneous fermentations have inconsistent or heterogeneous quality outcomes. However, fermentation managers procure to simplify the diversity of the environmental conditions and practices to decrease such heterogeneity. The practice of selecting fermentative environments or controlled facilities is common; for instance, people procure fermenting inside the house or special areas to control the external environmental heterogeneity in light incidence, temperature, external contaminants, or pathogens. Moreover, there is a cultural selection of the person who performs the fermentation and the substrate's quality [22,23,97,163,164]. A commonly overlooked aspect is how the microbial communities of starters are selected, prepared, conceived, stored, and used by local fermenters looking for the most favorable composition to improve the quality of their final products. Documenting such a process would give insights about how these communities of microorganisms are managed.

The interrelationships between the native microbial strains, substrates, techniques, tools, and fermentative environments of TMFB have been little studied. We identified studies that characterized the clay pots or tinas de fermentación for pulque [164] and **tesgüino** [85]. In fact, for **tesgüino** clay pots, fermenters use the specific name of tesgüineras and if the clay pot is broken, the pieces are trembled inside a new one, thus maintaining the microbiota from the old one. Nevertheless, few studies have attended to the importance of these containers as reservoirs of microbiota and their relevance in the fermentation process.

How Diverse Are the Inconspicuous Microbial Environments?

As mentioned, most studies on microbial environments in fermented beverages have been conducted with culture-dependent methods, isolating the most common microorganisms, among them *S. cerevisiae*, as the main microorganism responsible for alcoholic fermentation. These are invariably present in **mescal** and **pulque**. Nevertheless, for maize fermented beverages, the isolation and characterization of microorganisms have been directed to bacteria to characterize the possible probiotic functions of lactic acid bacteria (LAB) and, more recently, their function as a source of nitrogen fixation bacteria [163].

We found that only 10 beverages have been studied to characterize their microorganism communities, identifying 255 species of microorganisms. **Pozol** (Poz), **pulque** (Pul), and **mescal** (Mes) are the beverages with more species recorded (Table S2). This could be partially explained because a larger number of studies have been carried out on these beverages as also shown in the conceptual network (Figure 2). The network analysis reveals low connectivity that may be explained because there is high specificity in microorganisms in some of the beverages (Figure 3). In addition, it shows numerous links per species since genera such as *Lactobacillus* (Lac), *Bacillus* (Bac), and *Saccharomyces* (Sac) are shared among most groups of beverages. The network values are shown in Table 2.

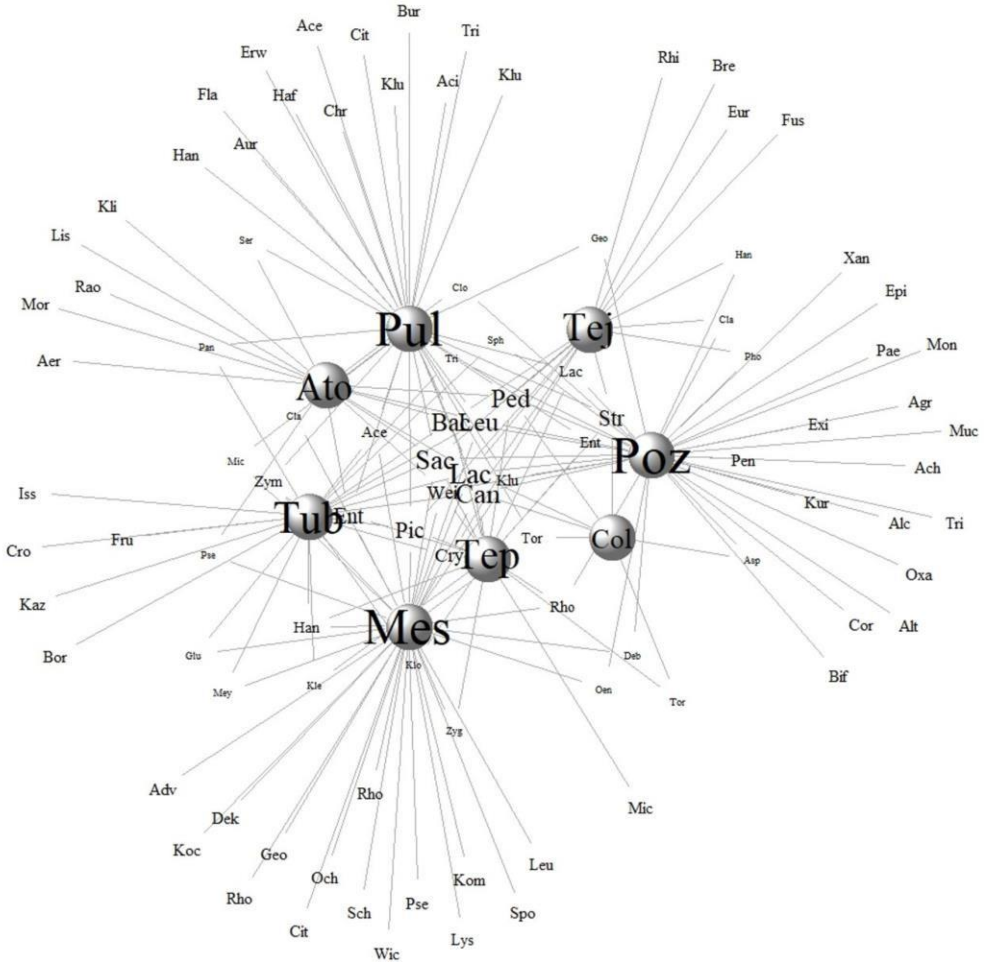

Figure 3. Network of microorganisms. Grey circles represent the names of the TMFB, Tep is for **tepache,** Col is for **colonche**, Mes is **mescal**, Ato for **atole agrío**, Pul for **pulque**, Tub for **tuba**, and **Tej** for tejuino. The size of the letters represents the number of microorganisms recorded for each beverage. The letters in the middle represent the microorganisms that are shared commonly in the studied beverages. *Saccharomyces* (Sac), *Lactobacillus* (Lac), and *Candida* (Can), among others, are common shared microorganisms. **Mescal**, **pulque**, and **pozol** are the most studied beverages in which a major group of microorganisms has been recorded. **Colonche** displays the lowest connectivity due to the few studies on this beverage. The genera of microorganisms and the names of beverages are displayed in the Table S2.

Through the nested analysis, we can see that **mescal**, **pulque**, **atole agrio**, and **pozol** are the beverages with the highest number of microorganism species identified, while **colonche** is the beverage with fewer genera identified. In general, six modules of microorganisms in TMFB were detected: (1) **mescal**; (2) **pulque**; (3) **atole agrio**; (4) **pozol**; (5) **colonche**, and (6) palm and **tepache.** This analysis shows that 99 species occur in the most studied fermented beverages, which might be the generalist core of microorganisms intervening in these fermented products. Interestingly, with this analysis, we identified that **pozol** has 24, **mescal** 23, **pulque** 22, **atole agrio** 10, and **colonche** 2 genera with low shared similarities with other beverages, and those could be specialist genera in each traditional beverage. Nevertheless, as the production practices and substrates vary for each event of production and ferment type, further analyses are needed for more precise information.

Forthcoming technologies such as CRISPR/cas9 [167–174] or the improvement of specific strains [115,156] could play important roles to improve these products as it has happened with yeast from *S. cerevisiae* in the fermentation of several products [172,173]. Nevertheless, careful studies should be performed about how and when these microorganisms are or can be intentionally used in these beverages because there is not a clear panorama about the ecological implications of using these microorganisms in replacing local native microbiota.

3.6. Uses of Fermented Beverages by Human Cultural Groups and Future Directions

Mestizo people produce and consume most of the TMFB, mainly those prepared with maize and agave as the main substrates. This could be explained because mestizo people are the most numerous in Mexican society and have recovered Indigenous traditions; also, because maize plays the key role in Mexican gastronomy, it is widespread, and fundamental in the local communities' nutrition [175,176]. These facts also explain that maize is the most generalist substrate of TMFB and the key role of these beverages in social cohesion, festivities, and ceremonies, such as tesgüinadas [177,178]. Likewise, many of the TMFB that have been recorded are used as medicine to prevent diarrhea, reduce infections, constipation, and, in general, to improve health. These beverages are currently part of daily life food, refreshing beverages during the working hours, and part of local ceremonies.

Indigenous cultural groups are interested in looking forward and renewing their connections with their lands and cultural heritage and recovering their traditional foodways to regain cultural strength and personal and community health [30,179]. This could be visualized in numerous forms of research that have identified how communitarian leaders and elders have encouraged youth to learn about harvesting and how to prepare their traditional foods around the world. Combining knowledge from different sources and epistemic systems is necessary to understand the diversity within and across ecological, social, and cultural systems, which are important factors underpinning conservation and natural resource management strategies [179–181]. This should be a particular concern in the case of traditional fermented beverages around the world, not only in Mexico.

It is important to highlight the marked level of segregation of the Mexican Indigenous people, which has been verified by numerous anthropological and socio-demographic studies based on synthetic demographic and poverty indexes [182–185]. Figure 4C shows a clear correspondence of TMFB with cultural groups. Most of them correspond to the mestizo group in the central region of Mexico. It should be considered that Indigenous people are not a homogeneous sector. The censuses of the Mexican population report gradients from monolingual to bilingual speakers [185], and numerous studies show that most Mexican people have extraordinary mixtures of Indigenous and non-Indigenous cultural aspects. However, it is generally recognized that Indigenous people are one of the sectors living in extreme poverty with no access to education and health services. The lack of monetary income and household goods and social marginality are factors eroding Indigenous cultures, pushing people to migrate from their original areas to cities, where Indigenous languages and culture are often discriminated [185]. This process endangers the maintenance of general culture and the transmission of the traditional knowledge on the production of fermented beverages.

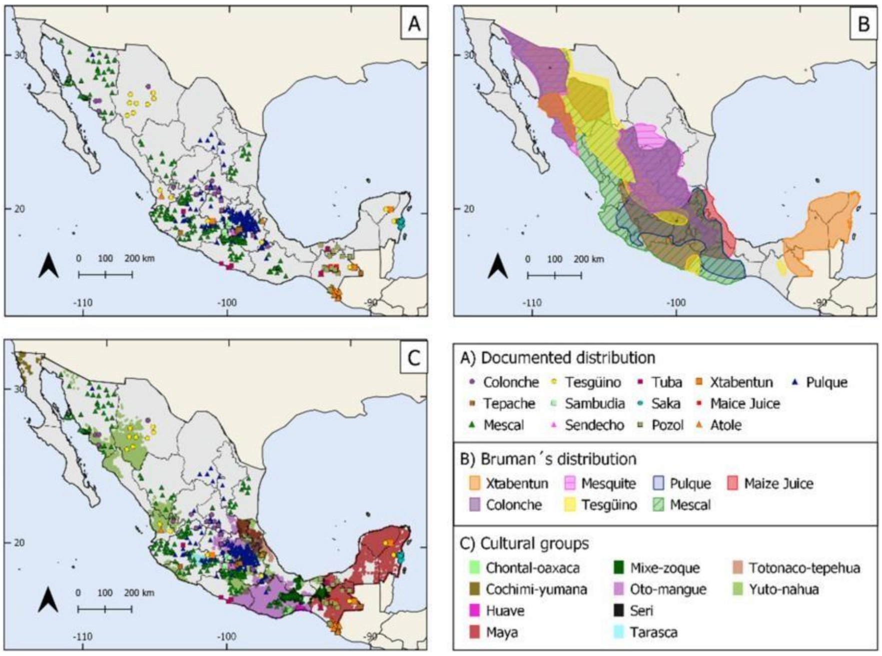

Figure 4. Maps of distribution of TMFB: (**A**) documented distribution of the TMFB; labels are indicated in the low right rectangle; (**B**) distribution proposed by Bruman; (**C**) distribution of TMFB according to the current review and cultural groups grouped by language.

Efforts should be directed to characterize and document aspects of TMFB, such as their uniqueness, human cultural specificity, their heritage status, the dietary patterns, their role in cultural identity, practices in the agricultural production of raw materials for fermentation, dishes and gastronomic innovation, preparation techniques, recipes, food traditions, symbolic dimensions, and material aspects such as utensils and dishware, among other biocultural topics. In addition, promotion activities would be relevant. For instance, promoting events in the communities, sponsored through schools, councils, andcultural centers, can be effective to illustrate, highlight, and demonstrate the values of traditional food systems [186,187]. These activities could help to maintain this marginalizedbiocultural heritage.

3.7. *Reviewed Distribution of the TMFB*

We compared the distribution of TMFB documented by Bruman in 1993 (Figure 4B) with information documented in this review (Figure 4A). We overlapped both maps to visualize the localities where these beverages could be produced nowadays and, accordingly, should be attended as priorities in further studies (Figure 4). It can be noticed that Bruman reported 7 beverages and we found 15, adding specific sites of **tepache**, **sendechó**, **sambudia**, **atole agrio**, **saká**, **tuba,** and **pozol** distribution.

The most striking result is the current absence of mention of a traditional fermented beverage made with mesquite pods reported by Bruman and a beverage named **bingarrote** or **bingui** from central Mexico, reported by Pineda [52], which was prepared with underground cooked and then crushed maguey stems; this material was placed to ferment into a pulque container, and afterwards the fermented liquid was distilled in an alembic. The ferment is called **binguí** or **benjuí** and the spirit **bingarrote**. It is a sort of culinary hybrid between pulque and mescal, but it is unclear which agave species was used. This information could be crucial to recover this apparently lost food, which could be a lost knowledge to humanity [188–191].

A first sight of maps in Figure 4 suggests that there has been a dramatic reduction in the production and consumption of the traditional fermented beverages, since Bruman defined areas in the early 1990s until the current research. However, it is important to emphasize that Bruman's methodology was mainly based on his expert knowledge and data that he collected through fieldtrips. We identify that the locations recorded in our review represent shorter areas due to the following reasons: (1) there is a gap in the research on uncommon traditional beverages contrasting with that on **pulque** and **mescal**, (2) there is a systematic oversampling in the same localities for most of the studies; for instance, five **pozol** studies are performed in the same locality and this fact does not allow characterizing the potential area of this beverage, and (3) there has not been regular monitoring of the production of some of these beverages, and, consequently, it has not been attended before.

We therefore propose that deeper studies are still necessary to identify, characterize, and monitor the actual and potential production areas of TMFB. This task will require fieldwork, information about the distribution of the substrates related to each beverage, and a careful characterization of localities where it is produced, using approaches from ethnobiology and ethnography that could bring insights about the possible processes of cultural erosion and the effects of market pressures and cultural discrimination over these marginal products. Such studies could also be the way to promote maintaining or the revival of these products [28,192]. The loss of traditional food systems will result in decreasing culture-specific food activities, thus influencing the decrease of dietary diversity [193]. Moreover, TMFB could be part of touristic development, reliable small-scale food markets, and local health strategies, but most of them remain unexplored and some others are in danger of extinction.

3.8. *How Are We Attending the Maintenance of This Intangible Biocultural Heritage?*

In recent years, the awareness to protect traditional relationships between humans and environments has promoted the development of systems of legal protection and biocultural management around the world [194]. Numerous challenges have arisen to protect genetic resources, intellectual property rights, and natural resources, among other important topics related to traditional local knowledge [195,196]. Studies have been directed to document the local knowledge systems in several countries to define what is local and global, traditional, and Indigenous, and the authenticity and origin, as well as different ways to interact with the environment and how to attend to environmental crisis issues [197,198]. Traditional food systems can play a key role in the strategy to combat malnutrition while ensuring sustainable development [199]. The Food and Agricultural Organization (FAO) now recognizes that food items such as fermented products must be considered important in areas where malnutrition is evident. Use and conservation are commonly associated issues; conserving traditional food is a powerful way to conserve biocultural heritage.

Food systems are part of complex bodies of knowledge, most of them constructed empirically [200] and transmitted in multiple verbal and non-verbal ways, such as know-how or learning-by-doing [200], and fermented products are not exceptions. These products have been embedded as part of the daily lives of many people, including those currently marginalized rural or Indigenous groups [201]. The diversity of fermented products is an outstanding reservoir of genetic resources that has high potential to obtain secondary products such as extracts, enzymes, dyes, and others compound that can be involved in global markets and could help to solve problems such as hunger [202,203] and poverty and may play a key role to reinforce cultural identity [12]. Nevertheless, several cases of the commodification and commercial use of local knowledge have been recorded, which commonly decontextualize and make inappropriate retribution, and contribute to disarticulate local communities [204–207]. Therefore, analyzing the conditions for fair trade are indispensable when analyzing sustainable ways of using these traditional resources and products. This is a particular concern in relation to the industrial **mescal** production, for instance.

The Mexican government signed the Nagoya Protocol in 2011 and was ratified in 2012. This is the major international regulation system about access to genetic resources and fair and equitable sharing of the benefits derived from their use, which emerged from the Convention on Biological Diversity. However, it was not until 2014 that the Nagoya Protocol was enacted as a supreme law in article 133 of the Mexican Constitution.

The main aim of this protocol is favoring incentives for the conservation of biological diversity, the sustainable use of its components, and the prevention of misappropriation of genetic resources and traditional knowledge on them, which is relevant for a bioculturally mega-diverse country such as Mexico.

Since Indigenous peoples hold traditional food system knowledge, interinstitutional and intersectoral initiatives would make more significant contribution to increase the potential of these resources, but local people should be protagonists. The documentation of traditional food systems is urgent since knowledge of food harvesting and preparation is rapidly disappearing. It is therefore crucial to enhance the public policies to support the maintenance of this traditional knowledge.

The conservation of species and varieties involved is equally important. Cultural historians, ethnobiologists, and the general public should become aware of the distinctive varieties of plants used as substrates for fermentation, their conservation, and recovery. For instance, the varieties of *Agave rhodacantha* classified by the Mayo people as San Antoneña and El Chino were used in the fermentation on an agave beverage called **yocogihua** in southern Sonora and northern Sinaloa. Most commercial production of mescal in this region blinked out during the Ley Seca that began in Sonora in 1916, but remarkably the persistence of these varieties was documented off and on from 1888 to 1965 when the last plantation of them was closed. Nevertheless, the Mayo who worked in the plantation rescued or dispersed them to rancherias neighboring the plantation in Masiaca, Sonora, thus several fencerow plantings of *A. rhodocantha* persist nearby, even though it is otherwise rare except for one other location in Sonora. The recovery of these cultivars and possible reintegration into the contemporary production of culturally distinctive fermented beverages in Sonora is now being undertaken [208,209]. As mentioned, **bingarrote** and **bingui** remain used for an analogous beverage today that is rarely produced in the state of Guanajuato where *A. salmiana* varieties are still in use for both pulque and mezcal production [209]. Identifying through community elders which varieties or species are currently associated with sporadic **bingarrote** and **bingui** production near San Miguel de Allende could help to rescue both the plant genetic resources and the traditional cultural practices historically linked to them.

For local knowledge associated with microorganisms, the situation might be overly complex and difficult to attend, as certain microorganisms are not cultivable and not easy to identify. The lack of a microorganism's accessions in collections, the low characterization of the selection mechanisms, and the implications of this selection over genetic and phenotypic traits in microorganisms can make the establishment of protective laws or conservation policies on this topic challenging. To understand the crucial roles of microorganisms on the TMFB process, we need to know their ecological niches, population dynamics, and relationships between microbiome and environments and microbiome and the selection process.

4. Conclusions

Mexico has a unique gastronomic culture characterized by its multiethnic, high biocultural diversity and long cultural history. Biological diversity is used in traditional Mexican cuisine, and, undoubtedly, Mexican fermented beverages are intimately associated with plant products that have been managed and domesticated in Mexico, as it can be seen in the relevance of fermented beverages based on maize, agave sap and stems, or cacti fruits. However, this is also the case of dozens of wild species that are involved in traditional beverages. Foreign technologies, tools, and plants have been integrated into the Mexican foodscapes, and this fact has promoted a diversification of beverages and a diversification of sensory qualities acceptable to a wide range of palates. TMFB are clear examples that traditional knowledge is a dynamic process that is constantly changing, adjusting, and evolving.

Traditional Mexican cuisine is an outstanding reservoir of genetic resources such as plants, animals, fungi, and, generally less considered, microorganisms such as yeast and bacteria which could play a relevant role for future nourishment applications. The TFMB are reservoirs of cultural diversity, practices, and worldviews of communities. However, studies have focused mainly on the biotechnological applications and on beverages of the *Agave* group, leaving apart other beverages that are rarely studied, thus limiting the action to combat the endangered permanence of these products and the local food systems. The study of fermented beverages under transdisciplinary approaches is fundamental to provide information to construct regulatory frameworks or proposals to protect the diversity that TMFB involves in maintaining the complex interactions between humans, plants, and microorganisms. We expect that these examples demonstrate how biocultural conservation and restoration can be tangibly integrated into the protection and promotion of the Mesoamerican gastronomic patrimony recognized by the UNESCO and the routes of research needed to achieve it.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/foods10102390/s1, Table S1: Plants involved in the production of TMFB registered in the literature. Grey boxes represent the presence of the specie and white boxes the absence. ***Ato*** refers to ***atole agrio***, ***Bal*** to ***balché, Col*** to colonche, ***Mes*** to ***Mescal***, ***Pox*** to ***pox, Poz*** to ***Pozol***, ***Sak*** to ***saká***, ***SaM*** to ***saMbudia***, ***Sen*** to ***sendechó***, ***Tab*** to ***taberna***, ***Tub*** to ***tuba, Tep*** to ***tepache***, ***Tej*** to ***tejuino***, ***Tes*** to ***tesgüino***, ***Cho*** to ***chorote***, ***Pul*** to ***pulque***. Table S2. Microorganism's genera previously registered in the literature. Grey boxes represent the presence of the genera and white boxes the absence. **Ato** refers to **atole agrio**, **Col** to **colonche**, **Mes** to **mescal**, **Poz** to **Pozol**, **Pul** to **pulque**, **Tej** to **tejuino**, **Tep** to **tepache**, **Tub** to **tuba**. The first three letters of the genera are displayed in the Figure 3.

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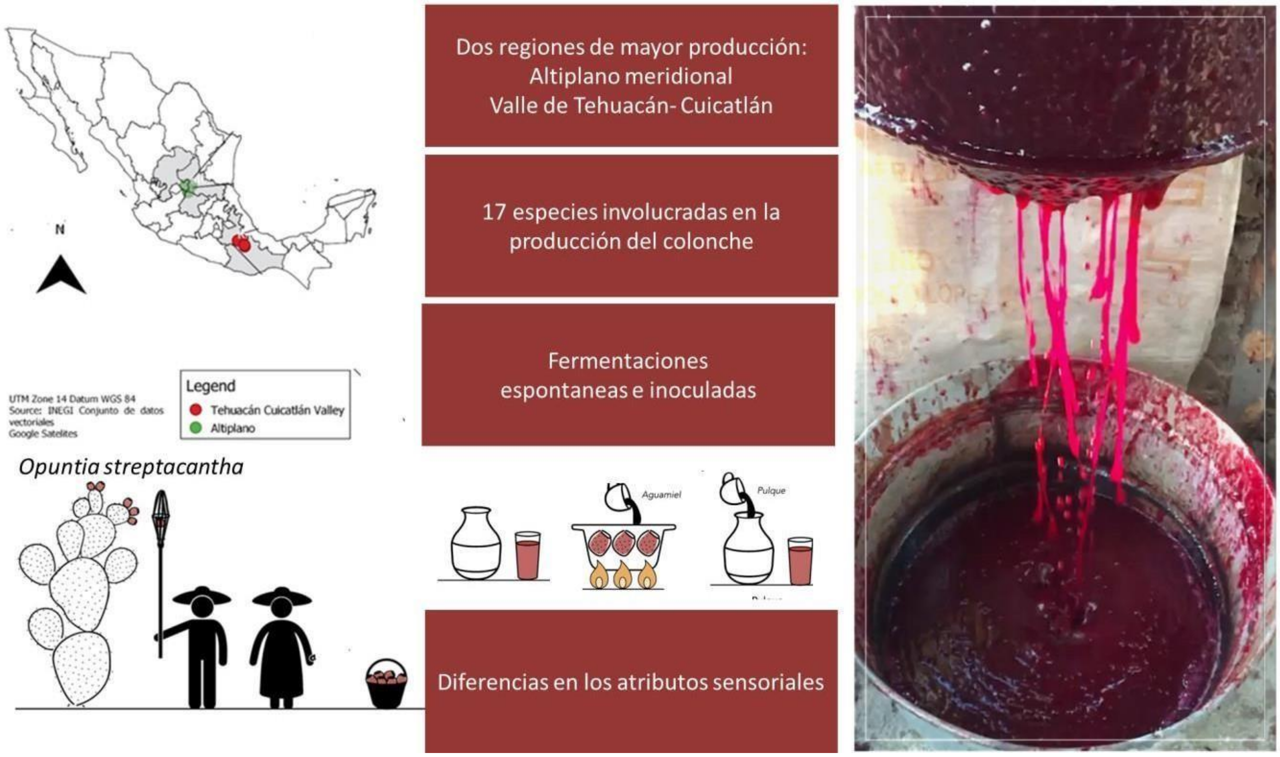
Capítulo 2

Traditional management of microorganisms in fermented beverages from cactus fruits in Mexico: an ethnobiological approach

Cesar I. Ojeda-Linares, Mariana Vallejo, Patricia Lappe-Oliveras, Alejandro Casas



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Traditional management of microorganisms in fermented beverages from cactus fruits in Mexico: an ethnobiological approach

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Abstract

Background: Fermentation is an ancient technique for preserving and improving the qualities of food and beverages throughout the world. Microbial communities, not seen by the producers of fermented goods, are the actors involved in the fermentation process and are selected upon through different management processes in order to achieve a final product with culturally accepted features. This study documented the preparation of "colonche" which is a type of traditionally fermented beverages made with the fruits from several cactus species in two main producing regions of Mexico, the Altiplano and the Tehuacán Valley. We documented the selection processes of the cactus species used and the practices that could influence microbial community composition, as well as, how the producers reach the desirable sensorial attributes of the beverages.

Methods: We conducted 53 semi-structured interviews and participatory observations with colonche producers in7 communities of the Altiplano and the Tehuacán Valley in order to characterize the practices and processes involved in the elaboration of the beverage. *Opuntia* and columnar cacti species used in colonche production were collected during fieldwork and identified. Selected sensorial attributes of *Opuntia* colonches were characterized by aranking table and visualized by principal component analysis in order to distinguish differences of this beverage in the Altiplano localities.

Results: Thirteen cactus species are used for colonche production in both regions studied. In the Altiplano, the most commonly used fruit is *Opuntia streptacantha* because it contributes to the preferred attributes of the beverage in this region. Selection of substrates by producers depends on their preference and the availability of fruits of *O. streptacantha* and other species. Fermentation is mainly conducted in clay pots which is perceived to be the best type of vessel contributing to the preferred sensorial properties of colonche. The two main differences in colonche preparation between the villages are the practice of boiling the fruit juice and the use of pulque (fermented sap of *Agave* species) as inoculum. The most contrasting sensorial attributes selected between localities are the alcohol content and sweetness, which might be in accordance with the practices used for obtaining the final product. Colonche is produced mainly for direct consumption and secondarily used as a commercialized good to be sold for economic gains contributing to the general subsistence of households. The preparation methods are passed on by close relatives, mainly women.

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Conclusions: Traditional producers of colonche use several techniques in order to reach specific sensorial attributes of the final product. The production of colonche has been upheld for generations but fermentation practices are divided into two categories; (1) the use of an inoculum (either from pulque, or from colonche saved from the previous year), and (2) the use of “spontaneous” fermentation. The differing practices documented reflect the contrasts in the preferred sensorial attributes between regions. Colonche is a beverage that contributes to regional pride, cultural identity and is appreciated because of its gastronomic value. Here, we argue that there is a clear relationship of human knowledge in the management of microbiota composition in order to produce this beverage. In-depth documentation of the microbiota composition and dynamics in colonche will contribute to the preservation of this valuable biocultural heritage.

Keywords: Columnar cacti, Ethnozymology, Fermentation practices, Foodways, Colonche, *Opuntia*

Introduction

It has been estimated that nearly one-third of foodand beverages in human diet involves fermentationprocesses [1]. Some fermented products are widelydistributed and support dynamic industries over a growing market for functional foods [2]. However,most of them are locally distributed in rural areasand are rarely seen or absent in urban contexts and markets. The ancient process of fermentation has been utilized for a broad spectrum of substrates dat- ing back to approximately 9000 years ago from pot- tery [3], but their use and management could have occurred even earlier.

Fermentation is an outstanding strategy enabling people to preserve foods as well as to transform edible raw matter into new products with unique sensorial properties [4, 5]. It also enhances the nutri- tional value of food and beverages that are prepared through fermentation processes representing an im- portant part of human nutrition in practically every food culture of the world [4]. Although the microbial relationship with food production, knowledge, health, and heritage, is highly important, relatively few stud- ies have been directed to characterize the microbial landscape that is composed of aggregated culinary and agricultural management decisions.

An understated aspect of ethnobiological studies is the knowledge and use of microbiota for traditional fermentation practices involving the autochthonous microbiota found on plant ingredients and from other naturalsources. Nevertheless, the transformation of raw mate- rials into value-added products could be assessed in avariety of ecological niches. Relatively scarce attentionhas been centered on plant attributes and management over fermentation practices to produce final products. Nowadays, the loss of this specialized knowledge is relevant because it is associated with the loss of biodiversity and practices associated with communities that use fermented foods to bolster food security, foster culturally important tastes, or anchor connections between food, identity, and health [6–8].

Given the implications of this lack of information, it is vital to extend empirical studies to different systems. Information on spontaneous traditional fermented beverages prepared and consumed in Mexico is scarce, mainly dominated by ferments of agave and maize. For example, in Mexico, “colonche” (also referred to as *coloche* and *nochoctli*) is a group of fermented beverages produced by fruits of different cactus species, which has yet to be documented in detail in published literature. Coloncheis a term resulting from the Spanish deformation of the indigenous Nahuatl term *nochoctli* which is derived from the words *nochtli* used for naming cacti fruits, and *octli* the term used for naming the fermented sap of agaves.

Fresh or fermented cactus fruits were widely con- sumed by indigenous peoples [9–12]. In particular,colonche was produced and consumed in pre- Columbian times by the indigenous peoples called “Chi- chimeca” by the Aztecs from the northern region of Mexico [13, 14]. In villages of the Tehuacán Valley, colonche is prepared with fruits of *Opuntia* and several columnar cacti species like *Pachycereus weberi*, *Escontriachiotilla*, *Stenocereus* spp., and *Polaskia* spp. [15–18]. Additionally, other types of fermented cacti fruit juices have been recorded in other regions and were consumed by the Aztecs and their tributary peoples from northern to southern Mexico [15–18]. In the Sonoran Desert and northwestern California, fruits, seeds, and ferments from saguaro, *Carnegiea gigantea*, and cardón, *Pachycereus pringlei*, were consumed by the Papago indigenous people [19, 20]. Fruits from these cacti were crushed and squeezed for juice, then, the fruit juice was boiled and ultimately fermented resulting in the product named “sa- huaro” [21, 22]. Although these wines do not receive the name of colonche, since the regional human cultures were not influenced by the Aztec, this beverage is clearly similar, and names are mainly generic. Nevertheless, scarce information is available on these beverages and the production of this traditional fermented beverage is decaying [23].

Plants of the genus *Opuntia* are the most abundant group of the Cactaceae family, currently spreadingthroughout the Americas, Europe, Asia, Africa, and Australia [24–26]. The cactus prickly pear fruit is oval elongated berries, with thick pericarp, juicy pulp withnumerous seeds, and a semi-hard rind with thorns. The pericarp and edible pulp may have different colors suchas green, greenish-white, canary yellow, lemon yellow, orange, red, cherry-red, or purple hues [27–29]. Prickly pears have long been known in traditional medicine for treating several pathologies such as ulcers, dyspnea, and glaucoma, as well as liver illnesses, wounds, and fatigue [30, 31]. Recent studies have found that juice from red prickly pear fruits has anticlastogenic potential becauseof their high number of antioxidants [32]. In addition,columnar cacti have been recorded as an important source of water, food, vegetables, and medicine [33].

In order to address the knowledge and use of micro- biota in traditional fermentation practices, we examined the variation of processes involved in colonche produc- tion in two regions of Mexico. The selection of fruits, fermentation practices, and sensorial preferences was registered. We selected the traditional fermented bever- age known as colonche because it is distributed through- out different regions, it is poorly studied and has been registered as a beverage at risk of extinction [34]. Colonche will allow us to compare the importance of traditional knowledge of fermentation in several localities because it is thought to vary depending on localcultural preferences. Our study looks to test the predic- tion that traditional ecological knowledge of fermenta- tion practices is still in effect today but in decay. Additionally, our aim is to show that final fermented products are shaped by the selection of substrates, prac- tices, tools and that the quality of these products is cul- turally shaped and based on sensorial attributes.

Materials and methods

Study area

Local stakeholders were identified in three localities of the Altiplano region and four communities of the Tehuacán-Cuicatlán Valley region. The snowball method was followed in order to identify colonche producers in each locality. Producers who gave their permission were then interviewed. In the Altiplano region, we studied the communities of Laguna de Guadalupe (LG), in the state of Guanajuato, Mexquitic de Carmona (MC) in the state of San Luis Potosí, and Pinos (PZ) in the state of Zacatecas. In the Tehuacán-Cuicatlán region, we studied the communities of Los Reyes Metzonla (RM) and Coxcatlán, in the state of Puebla, and Quiotepec and Cuicatlán in the state of Oaxaca (Fig. 1). The climate in both re- gions is semiarid and characterized by a cold winter anda hot summer. The vegetation is predominantly xero- phytic and dominated by arborescent cacti (mainly*Opuntia* spp. and columnar cacti) [35]. The Altiplano

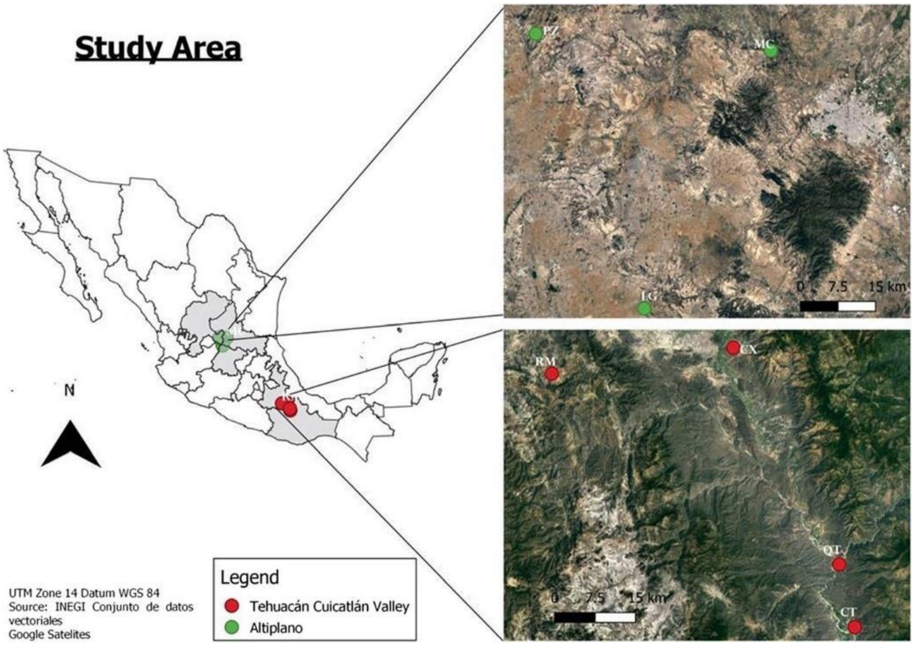

Fig. 1. Study area in Mexico, grey regions comprise states where colonche production has been documented. Red points are sites where information was collected in the Tehuacán Valley; green points belong to the Altiplano localities. The map was elaborated with an open-source software, Qgis3.4, https://qgis.org/es/site/. Source: INEGI conjunto de datos vectoriales

region was historically called the "Tunal grande," a term that refers to the high availability of cactus prickly pear fruits, whereas the vegetation of the Tehuacán Valley is predominantly columnar cacti forests [36].

Ethnobiological study

We performed semi-structured interviews and participatory observations in order to document the preparation process of colonche, the different plant species sub- strates, sources of inoculation, and control of microbiota responsible for fermentation. We also documented information about the economic role of colonche production in households, the purpose of preparing this beverage,the most important attributes valued in their final prod- uct, and socio-cultural data related to the consumption of colonche. The semi-structured interviews were guided through a questionnaire (Additional file 1), including the following topics: (1) general information about producers, (2) the production process, emphasizing prac- tices for fermentation (3) tools, instruments and techniques employed, (4) species involved providing sub- strates, (5) availability of plant substrates (fruits available in the neighboring territories), and (6) perception about sensorial attributes of colonche. In relation to the latter topic, information was obtained by inquiring directly to rank the importance of traits.

Sampling

Fifty-three colonche producers were interviewed. Thirty-one of the producers were located in three localities of the Altiplano during the production season (August-September), 71% of the producers were elder people (40 to 70 years old). The remaining 22 producers were lo- cated in four communities of the Tehuacán-Cuicatlán region (in April and May) (Table 1). Finally, a principal component analysis (PCA) was performed to characterize the most valuable attributes in the final product for each locality; this analysis was performedthrough the Rstudio software.

Botanical collections

Opuntia and columnar cacti species used for colonche production were collected and identified by local members of the communities studied. Then, *Opuntia* species of the Altiplano region were identified with the help of Dr. Antonio Reyes-Agüero from the Autonomous University of San Luis Potosí, an expert in *Opuntia* taxonomy. The columnar cacti species were identified byour research team.

Results

General information of colonche producers

Colonche production in LG is mainly produced by men, while in MC production is predominantly carried out by women (Table 1). In order to avoid noise in the data, the information from the PZ was removed from our study because of the low sample size and unclear pro- duction methods.

Colonche producers in the Altiplano region stated that the beverage is mainly consumed by family members and secondarily sold representing a small source of in- come (less than 10% of their total income during *Opun- tia* fructification. Colonche has such high value that consumers have found ways to store and transport the beverage to the USA and other regions of Mexico, with the main purpose to share with members of theirfamilies.

It is important to highlight that most of the producers learn the production process from their mothers. Also, new producers argue that it was a beverage that their family ceased to produce due to the absence of the mother. Nowadays, they have, once again, began to produce colonche because of its symbolic association with family relations. However, as a main threat for continuing colonche production, the producers interviewed identified the disinterest in colonche production and consumption by the young people, mainly because "it represents more work" and it is not easily available as other beverages like beer. Above all, producers preferred colonche consumption and recognize that the attitude

Table 1. Number of producers interviewed in both regions

Region	Community	Men	Age	Women	Age
Altiplano	Laguna de Guadalupe (LG)	7	> 40	1	> 40
		2	< 40	4	< 40
	Mexquitic de Carmona (MC)	3	> 40	6	> 40
		2	< 40	3	< 40
	Pinos (PZ)	2	> 40	1	> 40
Tehuacán Valley	Los Reyes Metzontla (RM)	3	> 40	2	> 40
	Coxcatlán (CX)	4	> 40	1	> 40
	Quiotepec (QT)	4	> 40	3	> 40
	Cuicatlán (CT)	3	> 40	3	> 40

upheld by the younger generations and the substitution of colonche for other beverages like beer endanger the continuation of the production of this historic product.

Colonche is not considered as a medicinal beverage in most of the communities, only 7% of the respondents considered that it has health benefits related to lungs and stomach illnesses, while most of the respondents said that they were not aware of health-related benefits.Most of the respondents consider that colonche has eu- phoric attributes due to its alcohol content.

In MC, colonche consumption occurs mostly during Sunday's market; therefore, the production of colonche begins Wednesday. Each household produces at least 20 L to bring to the Sunday market. Unlike MC, colonche in LG is locally consumed within their households and shared with friends and guests. However, a recent festival named "feria del colonche," which takes place in LG during September has proven to be a very successful way to popularize and share colonche in the region and generate incomes for local producers.

In all villages of the Tehuacán-Cuicatlán Valley, colonche is produced for direct consumption by household members, family meetings and parties. Additionally, colonche is a sub-product associated with the extraction of the seeds of *P. weberi*, which are highly valued in regional markets [37, 38].

Substrate selection

A total of seven *Opuntia* species and varieties and six columnar cacti species are used for colonche productionin both regions. However, as mentioned above, *Opuntia streptacantha* is the main ingredient of colonche pro- duced in the Altiplano region and *Pachycereus weberi* in the Tehuacán Valley. Nevertheless, all the communities add fruits of other *Opuntia* species when fruits of *O. streptacantha* are not available. The other species of cactus prickly pears used for colonche production include *Opuntia orbiculata*, *O. robusta*, *O. hyptiacantantha*, *O. phaeacantha*, and *O. ficus-indica*. In particular, in LG, *O. streptacantha* is widely distributed in managed and unmanaged landscapes and producers invest at least 2 h (± 30 min) daily for fruit collection. In contrast, in MC, *O. streptacantha* is not widely distributed and is onlyfound in private managed properties; as a result, pro- ducers propagate *O. streptacantha* by using cuttings, young plants, and cladodes to establish plants near their houses or within their gardens. If producers of colonchedo not directly collect *O. streptacantha* fruits they pur- chase or exchange colonche with local growers for ac-cess to fruits. In contrast, fruits are widely available inPZ but, nowadays, is rarely produced. In fact, production in PZ was not well characterized because of the lack of producers and information in this region.

In the Altiplano localities, *Opuntia* prickly pear fruitsare collected with a sickle and peeled with a knife in situ. Then, the peeled fruits are placed in plastic containersand transported to the house of the colonche producer. Harvesting can include all family members, and it is performed in the morning to avoid collecting fruits warmed by the sun. Ripe *Opuntia* fruits are selected for colonche production. Non-ripe fruits have less sugar content andare typically not preferred. If non-ripe fruits are used,more fruits must be collected in order to produce colonche with the same flavor quality. Additionally, red fruits are favored for colonche production, however, when red fruits are scarce, yellow and white fruits couldbe added resulting in changes in flavor, color, and tex-ture (Fig. 3a).

In the Tehuacán Valley, people from Quiotepec and Coxcatlán prepare colonche (also called "pulque rojo" or "red pulque") mainly with fruits of *Pachycereus weberi* or cardón, *Polaskia chichipe*, *Escontria chiotilla*, *Stenocereus stellatus*, *S. pruinosus*, and *Opuntia pilifera*. Fruits of these species are produced from late January to early May, the peak of fruit production occurs in April. The exceptions are *Escontria chiotilla* and *Stenocereus stellatus* which have fruit production peaks from July to September. In Cuicatlán (Cu), people use the fruit of *Opuntia pilifera* for preparing colonche. In this town, as well as in Quiotepec (Qu), and Coxcatlán (Co) people commonly use fruits of *E. chiotilla*. They say they occa- sionally prepare colonche with fruit of *S. pruinosus* and *S. stellatus*, but they say these fruits should be ripe, otherwise, the colonche would be bitter and sour. People said they also have tried colonche preparation with the fruit of *Hylocereus undatus*, and *Lemairocereus hollianus* but they do not like neither the insipid flavor nor theviscous texture of colonche resulting from the fruit ofthese species. In San Luis Atolotitlán (SLA) and Metzon- tla (Mz), people more frequently use fruit from *E. chio- tilla*, *P. chichipe*, *P. chende*, *S. stellatus*, and *S. pruinosus*.In all cases, seeds are removed, but only recovered for consumption and commercialization the seeds of *S. prui- nosus* and *S. stellatus*, particularly those varieties produ- cing larger seeds. People gather cardón fruits by using a "chicol," which is a long stick, commonly a "carrizo" stem (*Arundo donax*), whose extreme is cut into strips which are doubled and tied with a wire or palm fibers to form a basket, which is appropriate to pull the fruit down the cardón branches without causing damage to cactus plants.

All of the producers at the Altiplano quantify the yield of two plastic buckets of 25 L of peeled cactus prickly pear fruits that allow obtaining 15 ± 2 L of colonche. Whereas in the Tehuacán Valley, yields are similar, a 20-L bucket of peeled fruit may yield 16 to 17 L of juice, most probably because seeds of columnar cacti are smaller than those of *Opuntia* fruits. After being collected, fruits are carried from field to homes in buckets, where these are peeled outdoors and then pressed using a cloth, in order to separate juice and seeds, thus catching the seeds.

Production process

Figure 4 illustrates the general process of colonche production and differences in both regions and localities. As mentioned above, in the Altiplano region *Opuntia* prickly pear fruits are collected and peeled in situ in the morning and transported to the houses by the colonche producers (Fig. 2a), then the peeled fruits are left out- doors exposed in plastic buckets (Fig. 2b). Undoubtedly, this exposure would facilitate the colonization of micro- organisms for the fermentation process (Fig. 2c). Peeled fruits, slightly crushed by hand, are placed inside the clay pots in the evening every day (around 18:00 to 20:00 h), then the fruits are left to ferment in clay pot (Fig. 2d).As a safety practice, hands must be dried and cleaned without soap as the water and soap contaminate the colonche. The fermentation of colonche will be de- scribed in more detailed in the following section.

During the fermentation, clay pots are placed outdoors and covered with a thin cloth (Fig. 2e). Sometimes, clay pots are placed inside their homes during the night in order to maintain a constant temperature. If raining, clay pots are covered and moved to dry places. After the fermentation is completed, the seeds are removed with asieve and colonche is freshly served. Colonche is storedin plastic buckets inside producer households and locally distributed (Fig. 2f). Part of the colonche batch that is not consumed fresh can be stored in plastic bottles and may include a mixture of several items as 2 L of colonche for 1 L of alcohol, pineapple, cinnamon, raisins, and anise.This mixture can be saved for multiple years or sold as “vino de tuna” or cactus prickly pear wine. Cactus prickly pear wine is a way to enjoy colonche during the part ofthe year when fresh colonche is no longer available. But, itshould be mentioned that the process to make the “vino de tuna” significantly changes many sensorial attributes in comparison to fresh colonche.

In contrast to the Altiplano region, producers from MC invest more time and resources for colonche pro-duction, and this process varies among localities. Out- side the center of MC, producers boil the fruit juice three times during the preparation process, while the producers in the center of MC only boil the cactus prickly pear fruits one time. Additionally, in this region, prickly pear fruits from different cactus species are in- cluded in the mixture (Fig. 3a). Boiling is performed in metallic drums (Fig. 3e), and wooden tools are used tostir the fruit juice while boiling occurs. We recorded that the same wooden tools have been used for colonche

Fig 2. Colonche production at Laguna de Guadalupe (LG), Guanajuato. a Fruit harvesting. b Peeling the fruits in situ and transportation. c Peeled fruit storage. d Crushing and placing the fruits inside the clay pots. e 12 h fermentation inside the clay pot. f Colonche ready for consumption

Fig. 3 Colonche production in Mexquitic de Carmona (MC), in the state of San Luis Potosí. a Yellow cactus prickly pear fruits used when *Opuntia streptacantha* fruits are not available. b Stored concentrated juice for the following productions. c Woodburning stove with opuntias and agave as fuel. d Strainer for seed removal. e Metal drum used for colonche boiling. f Production site outside the house

production through several generations (80 ± 30 years) (Fig. 3f). Cooking time is not standardized and depends mainly on observations and criteria of the person preparing the product. Boling is performed over a fire from dried agaves and *Opuntias* (Fig. 3c).

The first boiling step allows for the separation of the prickly pear pulp and seeds. The seeds are then removed with a sieve (this is a key step because if seeds are present for the second boiling the product will have a smoky flavor). In a second boiling step, spices are added to give the final product the desired flavor profile. The most common spices used are *Cinnamomum* sp. and *Pimpinella anisum*. After boiling, the juice is filtered to remove the remains of the spices (Fig. 3d). The final boiling step is performed in order to concentrate the sugars. The juice resulting from the final boiling is called “la miel de la tuna” which means the honey from cactus prickly pear fruits. Finally, this concentrated juice can be stored in the fridge in plastic bottles or placed at the clay pot in order to begin the fermentation process (Fig. 3b). It is important to highlight that pulque is commonly used as a starter for colonche fermentation, and this is indeed added to start the fermentation in the concen- trated juice.

In the Tehuacán Valley, during the process of separating prickly pear seeds from the pulp, the fruit juice is collected in buckets or clay pots while seeds are rinsed with water and sun-dried. The fruit juice is stored in clay pots and covered, as all cases documented in this study. Then, a small amount of colonche from a previously prepared batch is added as inoculum of fermentation for the new colonche batch. Fermentation is carried out in dark cool rooms and the new colonche batch is ready to drink two or four days later. The fruit production seasonof columnar cacti is relatively long (3 to 4 months), and colonche may be prepared several times during this season. Seeds of cardón fruits are stored in dry places, packaged, and taken to the regional markets to be sold. People of the Tehuacán-Cuicatlán Valley highly value cardón seeds and typically combine them with chili pep- pers and green or red tomatoes to make sauces. Also,these seeds can be ground to a butter-like paste used for preparing several dishes, and it may be stored in the fridge to be used throughout the year (Fig. 4).

Traditional fermentation microorganism’s management

In all the cases studied, the fermentation of colonche occurs within clay plots. In most cases, the clay pot is a part of the household’s cultural heritage and is dated to about 80 years old or older. These pots are not glazed and, when cactus prickly pears fruits are not available, are primarily used for pulque production. Therefore, alayer of microorganisms might always be present in these clay pots. Producers point out that they prefer to produce the fermentation in clay pots rather than plasticor metallic containers because clay pots improve the fla- vor of the final product. Most of the fermentation occurs at room temperature (about 25 °C to 30 °C).

Fermentation at LG occurs mainly by “spontaneous” fermentation. However, in one case, an experienced

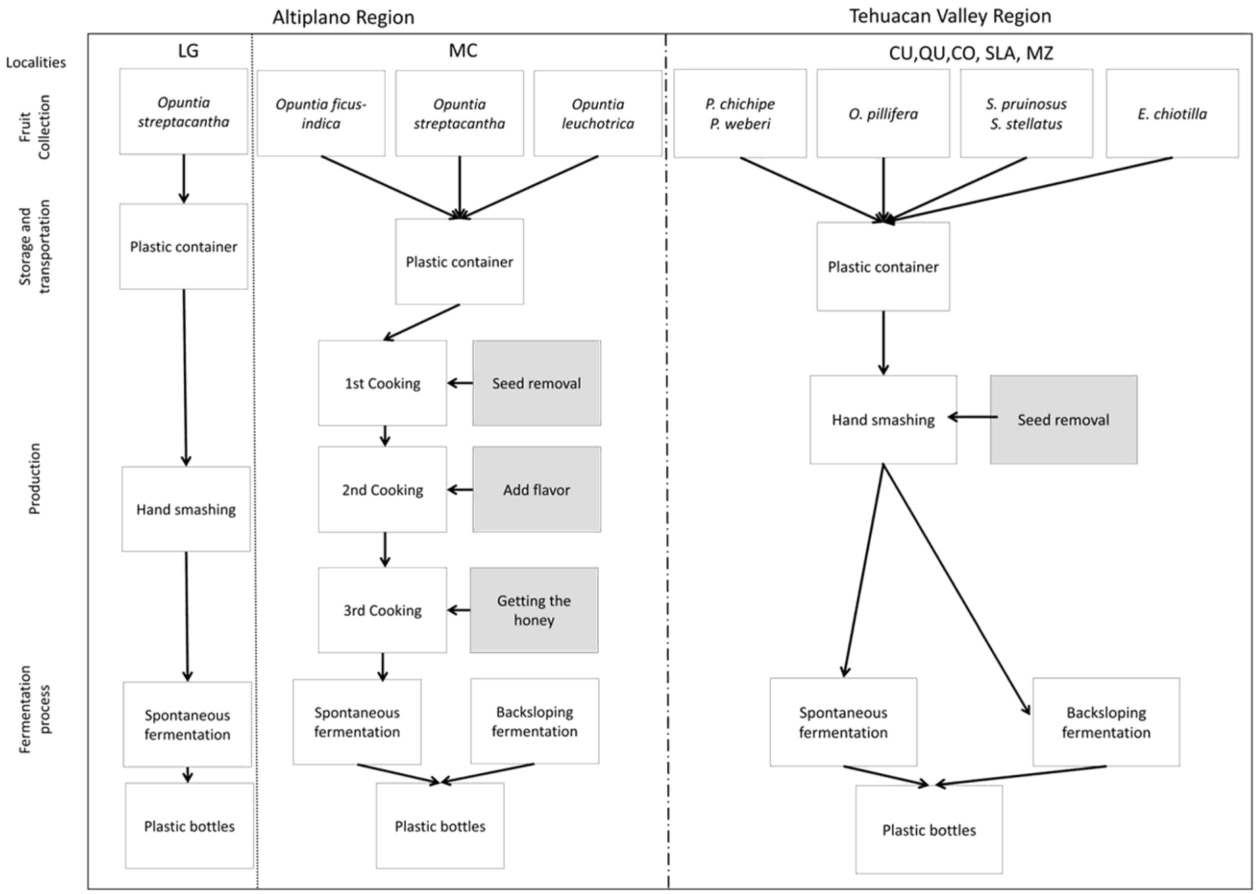

Fig. 4 General scheme for colonche production in both regions (Altiplano and Tehuacán Valley), and localities studied; Laguna de Guadalupe (LG), Mexquitic de Carmona (MC), Cuicatlán (CU), Quiotepec (QU), Coaxcatlan (CO), San Luis Atolotitlán (SLA), and Los Reyes Mezontla (MZ)

colonche producer prepares the first batch of colonche and then shares what is left of this batch to other pro- ducers as an inoculated strain known as "zinaiste" or "xinaiste" which guarantees a successful fermentation. The fermentation process lasts for 12 h in LG and 4 h in MC. Fermentation of prickly pear juice in MC starts with the addition of pulque from *Agave salmiana*. Therefore, in this locality, each producer creates their own xinaiste or inoculum. Pulque is added only to thefirst batch, the relationship is 15 L of concentrated juice and l L of over-pulque, which is called "pulque fuerte"by local people. The xinaiste could be stored in a fridgeor added to new batches. The fermentation in MC (4 h) is shorter than in LG (12 h) and could be due to the addition of the microbial community associated with the xinaiste or pulque.

As mentioned above, in the Altiplano localities, water is thought of as a contaminate of colonche, therefore,clay pots and other utensils used for colonche produc- tion most be completely dry. In other studies show that water modifies the composition and the dynamics of microorganism's communities in the fermentation process and can favor the production of acids [39]. Consequently, adding water to the colonche could bring undesirable flavors, modify the color of colonche from purple to brown and acidify the beverage. Careful strategies are carried out in order to store colonche without water. Cleaning occurs at the beginning and end of the season and is performed with only rinsing clay pots with water then sun drying (soap is not used because it has been observed to give a bad taste to the following batches). At the beginning of the season, most of the producers (80%) clean the clay pots with water and then dry them in direct sunlight. Other producers clean the pot with pulque or with a previously stored xinaiste andonly 2% of the producers add alcohol to the clay pots and light a match inside the clay pot using fire as a cleaning method.

When colonche availability declines, different strategies are employed to enjoy colonche for an extended period of time. For instance, in LG, colonche can be stored in glass bottles with the addition of alcohol and dried fruits. Producers in MC stored colonche in the fridge at − 4 °C. This method is similarly used in the villages of the Tehuacán Valley where it may be stored in refrigeration and at the end of the season it is com- monly kept in the freezer in plastic bags or bottles.

Selection of colonche desirable flavors

As mentioned above, the microbial community of each beverage plays a significant role in shaping flavor attributes (texture, acidity, etc.). These characteristics are selected by the producers and are modified by their practices and processes during the production of the colonche. An evaluation of the sensorial attributes was conducted by ranking from the most important to the less important, respectively. In order to visualize differ- ences between localities, a PCA scatterplot contrasted a priori groups. The results can be visualized in Fig. 5,with the attributes selected by colonche producers from the Altiplano region and the localities. The first axis rep- resents 34.47% of the variance while the second axis rep- resents 20.22% for a total of 54.69% cumulative variance.The attributes of the first principle component (PC1) are sweetness and alcoholic content which apparently gener- ate the highest variance, meanwhile, the attributes of the second principal component (PC2) are color and acidity which seem to explain the rest of variance observed. Clearly, this PCA allows us to separate localities prefer- ences which might be reflected by the differences in their fermentation practices between localities. Particu-larly, colonche in LG is a sweet beverage with higher al- cohol content. On the other hand, MC colonche is favored to have more complex sensorial attributes.

These results give us a glimpse of which microorganisms may be favored under the fermentation ofcolonche. This work does not directly compare the microbiota in different regions or localities. Further ex- ploration should examine the composition and the structure of the microbiota involved in fermentation in combination with the differences of substrates.

Discussion

The study of landraces of cultivated plants or rare breeds of livestock has played a central role in ethnobiological studies directed to document management and domestication. In contrast, relatively fewer studies have explicitly specialized in microbial ethnobiology. In this sense, documenting cultural and biological diversity through fermented food recipes, ethnobiologists have a chance touse fermentation to attend the interaction between humans and unseen organisms, the microbial communi- ties. It has been pointed out that fermented products are complex and peculiar expressions of local gastronomies; moreover, they often represent a part of local commu-nity identity [40]. In our study, we recorded that colonche production, consumption, and historical iden- tity differs among regions.

Traditional knowledge of fermented foods and beverage production has been recorded in studies around the world [7, 8, 41]. We registered the major role of men in the production of colonche, as the main participants in gathering fruits and producing the beverage. However, women are the main transmitters of knowledge of the practices involved in colonche production. This is thought

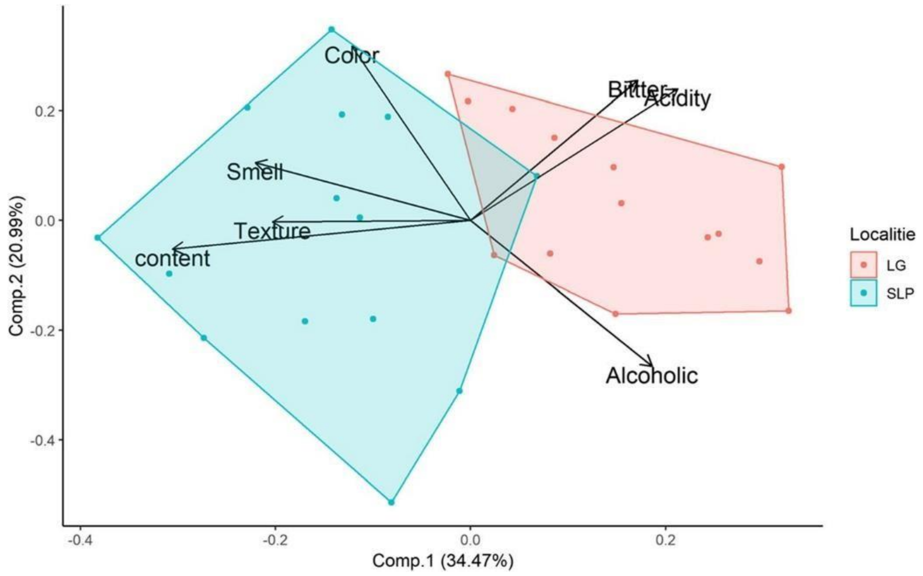

Fig 5. Scatter plot of PCA of sensorial attributes of colonche. Red points represent LG producers and green points MC producers. The axis represents, Principal Component 1 (34.47%) and Principal Component 2 (20.99%), which represent a cumulative variance of 55.46%. Groups of green and red points reflect the differentiation pattern of selection of the sensorial attributes of colonche in the two localities analyzed

to be due to the migration of men to other cities of Mexico or the USA. In the locality of PZ, the relatively low number of producers suggests that this beverage is soon to disappear from this locality. The renascence of the colonche tradition in the LG observed in the colonche festival has renewed the interest in consumption and production and has also resulted in a growing number of producers. The renascence of local fermented beverages is made possible by the active role of women, similarly as recorded in other studies [7, 8, 41, 42].

The main goal of the current study was not aimed to describe the health benefits of consuming colonche, but, there is a large body of literature that supports the idea that traditional fermented beverages have positive effects on health [2, 41, 43]. Undoubtedly, nutritional and health benefits of ferments are conferred by microorganisms involved in fermentation [44] and, in this sense, humans have been selecting favorable microorganisms and re- moving pathogen microorganisms by different strat-egies since ancient times [45]. Strategies may involvea spectrum of practices from spontaneous fermenta- tion to more specific strategies that control the condi- tions of fermentation [46–48].

For colonche production, we characterize the strat- egies such as; selecting specific places for the fermenta- tion, and the usage of temperature to concentrate sugars and flavors; as well as cultural practices like sharing the "seeds" of fermentation and inoculums among commu- nities. It is worth mentioning that the selection and experimenting of new substrates are active processes. For instance, in this study, we documented that people have experimented with preparing colonche with fruitsof *Hylocereus undatus* and *Lemairocereus hollianus*, which have been discarded because attributes of the resulting beverages are unsatisfactory.

The ecological impact of colonche production on populations of the species used is yet to be explored. However, it is possible to hypothesize that the impact is low. *O. streptacantha* is cultivated and enhanced in agroforestry systems, while *P. weberi* and *E. chiotilla* are wild species of long-lived arborescent cacti that become dominant in some columnar cacti forests. Previous studies of the population ecology of these species revealed that survival, not fecundity, is the most relevant demographic rate for the maintenance of populations near the equilibrium growth rate lambda [49].

In many cases, we observed in both regions the use of the technique back-slopping to in the fermentation process. Back-slopping is a classical way to improve and optimize the fermentation process by adding microor- ganisms that are well adapted to the fermentation mediato achieve tastier, safer, and healthier products [2, 50–57]. The practice of back-slopping results in the storageof starter cultures for colonche production to be later added to the prickly pear fruit juice. Back-slopping is a common practice for various fermented products, suchas sourdough, beer, and other fermented products. This idea is also linked to the interesting phenomenon of the co-evolution of the microorganism community in differ- ent fermented goods. It has been registered that whenthe microbial community is specific to a certain placeand type culinary preparations it may result in a longco-evolution between these microorganisms, substrates,and process [8]. Such is the case for some *Penicillium* species in the preparation of cheese [52]. Thus, one can imagine, these preparations may "express" a bio-cultural dimension of a given region or locality [8]. In this sense, we propose that strong and recurrent interactions of fer- ment good managers and microbial communities might represent possible pathways for the domestication of yeast and bacteria strains. But these processes should be investigated in more depth.

Traditional managers of fermented products do not necessarily name the microorganisms (as they commonly do for animals and plants), but, they do identify and describe with detail the preparation process and the sen- sorial qualities; taste, smell, and visual aspects [6, 53]. As we have shown, producers not only prefer different sen- sorial attributes in colonche but also perform active se- lection throughout the fermentation process in order to achieve such attributes. Additionally, the material of the vessel also influences the final product of colonche. When using a vessel not made from clay, colonche does not havethe same quality as is expected by the producers. Experi- mentation with different types of vessels and substrates tells us that the process of making colonche is still in ac- tive exploration. However, the selection of a specific sub- strate (*O. streptacantha* and *Pachycerus weberi*) by the majority of the producers explains that the selection of sensorial attributes may originate from the potential microorganisms associated with the traditional management of plant material.

Traditional knowledge of fermentation practices is minimal and seemingly undervalued even though this type of knowledge represents a very interesting combin- ation of diverse factors, like; location, practices, local flora, environmental conditions, and microbial taxa.Traditional knowledge also encompasses important cul- tural components. Mainly, we consider the decreasing transmission of this traditional knowledge from mother- to-son as the main threat to the existence of the prac- tice of making colonche. Particularly, in PZ, we ob- served that this is rapidly decaying and may be expected to be lost in a couple of generations. In con- trast, LG community is actively sharing the practices to prepare and consume colonche. Activities like colonche festival in LG greatly contribute to the preservation of microbial communities used for traditional fermentation, foodways heritage, and human wellbeing. These activities may be significantly supported by scholars and governmental and non-governmental agencies.

Conclusions

Management practices of fermentation are variable in colonche production, selection of the substrates and the final sensorial attributes of the beverage are different among regions and localities. However, even when microbiota is not seen by producers, the detailed manner in which they describe the preparation and the sensorial qualities such as taste, smell, and alcoholic content of colonche reflect a deep knowledge of the processes influencing fermentation. Our study hopes to build upon socioecological theory for in situ conservation of biodiversity and the cultural knowledge of traditional managers of fermented goods with the hope of encouraging preservation and promoting microbial refugia for these marginalized local foods. Fermentation management is a valuable biocultural heritage that deserves to be documented and protected. It offers the possibility of studying and analyzing the management and domestication processes of unseen organisms and the coevolutionary relationship between the substrates and the microorganisms involved in fermentation.

Supplementary information

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Additional file 1. Semi-structured interview for colonche producers

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Authors' contributions

COL designed the research semi-structured interviews, carried out fieldwork, analysis, and interpretation of data, and wrote the manuscript. MV conducted fieldwork and data collecting and map design. PLO read and commented on the manuscript and provided substantial bibliographic information. AC is the coordinator-supervisor of the main research project on plant domestication in Mesoamerica, participated in the conception of the study, and made substantial contributions to the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

Please contact the corresponding author for data requests.

Ethics approval and consent to participate

The authors declare that information in the community studies was consulted and informed in communitarian assemblies, local authorities, and people interviewed.

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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Capítulo 3

Constructing micro-landscapes: management and selection practices on microbial communities in a traditional fermented beverage

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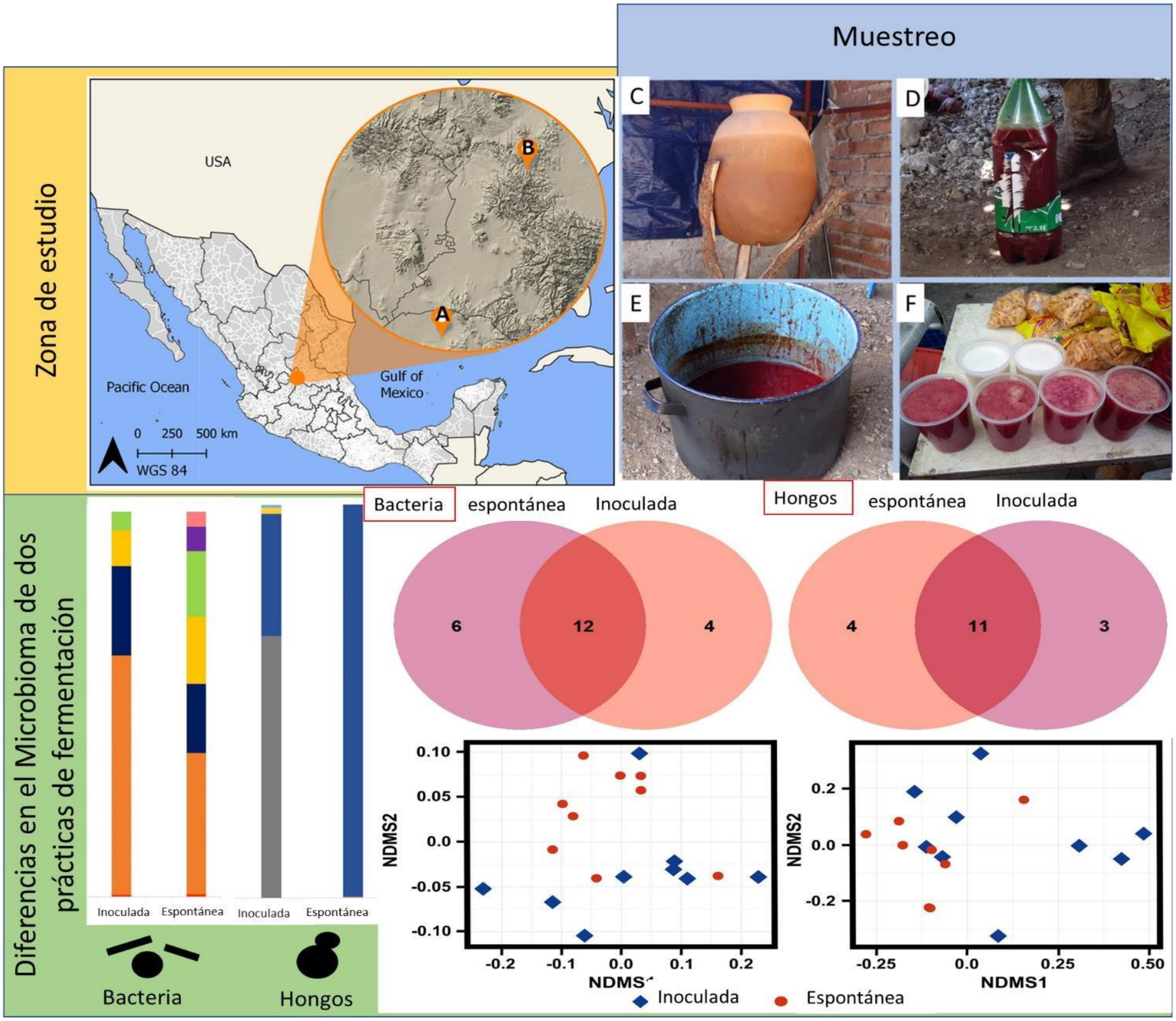

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Constructing Micro-Landscapes: Management and Selection Practices on Microbial Communities in a Traditional Fermented Beverage

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Colonche is a traditional beverage produced in Mexico by the fermentation of fruits of several cacti species. In the Meridional Central Plateau region of Mexico, where this study was conducted, it is mainly produced with fruits of *Opuntia streptacantha*; there, the producers perform spontaneous fermentation and/or fermentations through inoculums. Several factors can change the microbial community structure and dynamics through the fermentation process, but little attention has been directed to evaluate what type and extent of change the human practices have over the microbial communities. This study aims to assess the microbiota under spontaneous and inoculated fermentation techniques, the microorganisms present in the inoculums and containers, and the changes of microbiota during the process of producing colonche with different techniques. We used next-generation sequencing of the V3-V4 regions of the 16S rRNA gene and the ITS2, to characterize bacterial and fungal diversity associated with the different fermentation techniques. We identified 701 bacterial and 203 fungal amplicon sequence variants (ASVs) belonging to 173 bacterial and 187 fungal genera. The alpha and beta diversity analysis confirmed that both types of fermentation practices displayed differences in richness, diversity, and community structure. Richness of bacteria in spontaneous fermentation ($^0D = 136 \pm 0.433$) was higher than in the inoculated samples ($^0D = 128 \pm 0.929$), while fungal richness in the inoculated samples ($^0D = 32 \pm 0.539$) was higher than in spontaneous samples ($^0D = 19 \pm 0.917$). We identified bacterial groups like *Lactobacillus*, *Leuconostoc*, *Pediococcus* and the *Saccharomyces* yeast shared in ferments managed with different practices; these organisms are commonly related to the quality of the fermentation process. We identified that clay pots, where spontaneous fermentation is carried out, have an outstanding diversity of fungal and bacterial richness involved in fermentation, being valuable reservoirs of microorganisms for future fermentations. The inoculums displayed the lowest richness and diversity of bacterial and fungal communities suggesting unconscious selection on specific microbial consortia. The beta diversity analysis identified an overlap in microbial communities for both types of fermentation practices, which might reflect a shared composition of microorganisms occurring

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in the *Opuntia streptacantha* substrate. The variation in the spontaneous bacterial community is consistent with alpha diversity data, while fungal communities showed less differences among treatments, probably due to the high abundance and dominance of *Saccharomyces*. This information illustrates how traditional management guides selection and may drive changes in the microbial consortia to produce unique fermented beverages through specific fermentation practices. Although further studies are needed to analyze more specifically the advantages of each fermentation type over the qualityof the product, our current analysis supports the role of traditional knowledge driving itand the relevance of plans for its conservation.

Keywords: microbiota, management, ferments, ethnozymology, colonche, landscape domestication

INTRODUCTION

Throughout history, human societies have developed knowledge and techniques to use a plethora of species of plants, animals, fungi and other organisms from different ecosystems to satisfy nutritional needs (Campbell-Platt, 1994; Tamang et al., 2016, 2020, 2021). Interactions between people and nature commonly include a high diversity of management practices through which people adequate organisms and other components of ecosystems to secure their livelihoods; these practices are context-dependent on local conditions, outstandingly human culture and environment (Jones et al., 1997; Odling-Smee et al., 2003; Anderson, 2005). Traditional or local knowledge commonly includes complex bodies of information on the ecological context, relationships and behavior of the elements used as food, extensive repertoires of preparation procedures, as well as about their relationships with customs, taboos, rituals, and other cultural aspects (Nabhan, 2010; Tamang, 2010; Ratcliffe et al., 2019). All these biocultural facets can be visualized through the diversity of food products and practices related to it, and provide basic notions about what is edible, where and when edible elements are available, the way these should be harvested, and how they can be improved by cooking, roasting, fermenting, or making it harmless (Lévi-Strauss, 2012; Ratcliffe et al., 2019; Tamang et al., 2020, 2021; Tsafrakidou et al., 2020; Fernández-Llamazares et al., 2021; Gadaga et al., 2021; Kennedy et al., 2021).

Fermentation practices are part of the local knowledge and food systems, directed to procure and improve human health and wellbeing, but fermented products have changed the human food supply worldwide (Harris et al., 1989; Kuhnlein and Receveur, 1996; Steinkraus, 1996; Harris, 1998; Quave and Pieroni, 2014; Svanberg, 2015; Sõukand et al., 2015; Flachs and Orkin, 2019; He et al., 2019). Fermentation can contribute to construct sustainable food systems, diversify food production, and procure safety, security and sovereignty in human communities around the world (Johns and Sthapit, 2004; Marshall and Mejia, 2011; Ojeda-Linares et al., 2021). It allows preserving and improving nutritional value of food and conferring desirable properties to the final products such as textures and sensorial properties, whichare completely unlike to those of the starting materials (Smid and Hugenholtz, 2010; Smid and Kleerebezem, 2014). The microbial communities of bacteria, yeasts, and molds play a key role determining the quality of the fermented products, influencing their acidity, flavor, texture, nutritional value and other health benefits (Forssten et al., 2011; Todorov and Holzapfel, 2015; Gutiérrez-Uribe et al., 2017; El Sheikha and Hu, 2020). Changes in the microbial composition may be caused by variation in environmental factors, thus organoleptic and physicochemical characteristics of a fermented product could be modified and driven by managing fermentation environments through human practices (Escalante et al., 2016; Rebollar et al., 2017). The persons that perform and drive changes and follow the fermentation process in traditional contexts are recognized as traditional fermentation managers (Nabhan, 2010; Flachs and Orkin, 2019; Ojeda-Linares et al., 2020).

A common practice used to produce traditional ferments is the "spontaneous" fermentation, which involves microorganisms occurring in a local environment and is influenced by temperature, substrate type, techniques and tools employed, and other cultural factors that shape the composition and dynamics of the microbiota (De Vuyst and Vancanneyt, 2007; Vogelmann et al., 2009; Chaves-López et al., 2020). Due to the influence of all these factors, this type of fermentation is commonly assumed to be unpredictable, producing outcomes of inconsistent attributes; local people commonly have knowledge about how environmental and technological factors may influence the product and carry out practices to manage them, looking for decreasing the unpredictability of the resulting product. The other general practice is the use of starter cultures, which are characteristic for numerous fermented products around the world. Inoculation refreshment favors a periodically stable microbial community which provides an easy way to achieve optimal fermentations and desirable products (De Vuyst and Vancanneyt, 2007; De Vuyst et al., 2009; Brandt, 2014; Harth et al., 2016; Mukisa et al., 2017). Therefore, it is thought that this type of practice is associated with a set of selective forces favoring a specific community of microorganisms, guiding the dynamics and structure of the microbiota through the fermentation process (Vogelmann et al., 2009; Vogelmann and Hertel, 2011; Gibbons and Rinker, 2015; Liu et al., 2021).

The influence of human management over composition, structure and dynamics of microbial communities has been insufficiently analyzed, even when humans historically have developed numerous management techniques to direct, diversify and innovate the quality or to prevent the spoilage of fermented products around the world (Tamang and Fleet, 2009; Tamang et al., 2016). Ethnozymological studies have documented a wide range of activities that producers perform to adequate fermented products to their purposes; for instance, boiling the substrates, adding salt, plant, or animal products with antiseptic or flavoring roles are common practices (Quave and Pieroni, 2014; Hong et al., 2015; Sõukand et al., 2015; Pieroni et al., 2017; Álvarez-Ríos et al., 2020; Ojeda-Linares et al., 2021). Documenting the *known-how* of the management over the microbial communities in fermented products has high importance to understand the implications of human practices on the structure and dynamics of microbial communities during fermentation and to recover old human experience for innovation. In addition, this information provides elements to analyze possible processes of domestication at species and/or community levels.

Management includes a broad spectrum of practices that favor phenotypic attributes of organisms like size, flavors, colors, nutritional values, attributes to satisfy customs, rituals, ornamental, and other cultural purposes (Anderson, 2005; Casas et al., 2007). Through time, management has determined differences between wild and managed populations, the latter having higher frequencies of human-favored phenotypes. Such processes have been especially assessed in plant and animal populations where specific visible phenotypes are favored (Casas et al., 2007; Blancas et al., 2010). At ecosystem level, management practices may be directed to change species richness, diversity, and structure of communities and this is also an expressionof domestication, the landscape domestication (Casas et al., 1997; Smith, 2007; Albuquerque et al., 2019; Clement et al., 2020, 2021; Franco-Moraes et al., 2021). But, although the processes involved in ecosystem management are common and widespread throughout the world, these have been less studied than domestication at species populations level and even fewer are studies documenting management and domestication at micro-landscape level.

In this study we explored the general hypothesis thatthe composition and structure of the microbiota involved in fermentation would differ according to management practices. We expected to find a higher microbial diversity in techniques involving spontaneous fermentation than in those using inoculums, which would be favoring reduced consortiums of microorganisms due to continuous human selection. Such differences would also influence the dynamics of change through the fermentation of communities with higher and lower diversity toward less and more predictable products, respectively. Characterizing and analyzing the type and extent of change of microbial communities according to management practices are conceptually relevant to construct and test hypotheses abouthow these processes and techniques lead to domestication of microorganism consortiums and, probably, of specific lineages. Also, to design innovative strategies to improve food quality. Understanding how certain management practices do help to predict how diversity, composition, and richness of microbiota can be and change, would support principles of selection and management programs of microbial communities to obtain desirable products.

Such hypothesis has been narrowly explored, particularly because testing it requires methods and study systems able to compare and measure across confidently. A traditional fermented product prepared with the same substrate and different management practices represents an optimal study system for such purpose, while using High Throughput Sequencing (HTS) techniques allow detecting or rejecting associations between microbial composition and management practices. Currently, HTS allow glimpsing the composition and structure of microbial communities in different ecosystems (Metzker, 2010; Caporaso et al., 2011) and fermenting landscapes are not the exception (Foligné and Pot, 2013; De Filippis et al., 2017; Sha et al., 2018; Astudillo-Melgar et al., 2019).

To address our hypothesis, we selected the traditional fermented beverage called colonche. Colonche is a group of traditional Mexican beverages prepared since pre-Columbian times by the fermentation of fruits of several cactus species, including several species of *Opuntia* prickly pears and columnar cacti (Ojeda-Linares et al., 2020). We conducted our study in the Meridional Central Plateau region of Mexico, where themain substrate for colonche production is *Opuntia streptacantha*fruit. For its production, prickly pear fruits are gathered in wild and cultivated populations and stored in plastic trays almostevery day from August to October, when fruits are available. Local people carry out different fermentation practices, basedon spontaneous or inoculated procedures. To produce colonche through spontaneous fermentation, they harvest and peel the*Opuntia* fruits *in situ*, and then place them inside a clay pot wherefermentation occurs for about 12 h. In this area the colonche production is mainly performed by old men (60 ± 5 years old). The inoculated fermentation is performed by firstly boiling the fruits to concentrate their juice; then, the producers add thestarter cultures from previous batches and store the fermenting juice in plastic containers for 4 h (Ojeda-Linares et al., 2020). The production of inoculated colonche in the area is mainly performed by young women (32 ± 4 years old), and the production represents a recent recovery of this beverage by the younglings. Therefore, an analysis of the microbiota associated with this fermented beverage prepared with the same substrate under different fermentation practices is possible and wouldallow documenting how management over the fermentation process influences the microbial communities.

Nowadays, there is a worrying erosion of local food systems, causing the disappearance of traditional food products worldwide (Pingali, 2007; Turner and Turner, 2007; Johns et al., 2013; Albert et al., 2015; Hernández-Santana and Narchi, 2018; Akinola et al., 2020). Fermented products have been poorly considered in the analysis of erosion of local food systems, even when some of them have almost disappeared. Nonetheless, a renewed interest in their production has motivated studies and actions to guarantee its permanence (Madej et al., 2014; Svanberg, 2015; Cano and Suárez, 2020; Ojeda-Linares et al., 2020, 2021). In México, it has been recorded the loss of some traditional fermented beverages, even though the main substrates are available in the nearby, but the transmission of knowledge has been lost (Ojeda-Linares et al., 2021). The vanishing of fermented products not only favors disappearing fragments of foodscapes, but also the traditional ecological knowledge over fermentation practices, and therefore the efforts that humans have historically engineered to shape microbial communities and the evolutionary processes involved in making unique products.

This study aims to describe the microbial community of colonche under different management practices and highlights the relevance of traditional knowledge to construct the micro-landscapes and, in general, to preserve unique products thatare part of a local food systems. We aspire to contribute toa deeper understanding of the processes that can be involvedin the selection and domestication of microbial consortia and specific lineages of the microbiota. We also aspire to contribute to the conservation of traditional knowledge over fermentation practices and the establishment of a microbial panel helpful to determine the geographical origin of the product and supports the relevance and the way of its conservation.

MATERIALS AND METHODS

Study Area and Sampling

We studied colonche samples prepared by the fermentation of *O. streptacantha* fruits. We collected nine samples from spontaneous fermentations in the village of Laguna de Guadalupe (LG) in the state of Guanajuato, México from three different producers that performs similar practices. Also, nine samples of inoculated colonche produced by three producers in Mexquitic de Carmona (MC) in the neighboring state of San Luis Potosi (**Figures 1A,E**). We in addition collected samples of residuals from two clay pots one day before producers began spontaneous colonche fermentation. These clay pots have been used for almost 80 years for colonche production and are stored indoors when fruits of *O. streptacantha* are not available. Before the fermentation starts, the producers clean them only with water (no soap is added since according to people it changes the flavor of the product; **Figure 1B**). In addition, we collected and analyzed two samples of the inoculum, which were saved from the last production season, stored in a fridge and ready to usein the following batches (**Figure 1C**) and two samples of the cooked cactus prickly pear fruit juice before fermentation in the inoculated treatment (**Figure 1D**). The cooked samples represent a treatment that producers of the locality of Mexquitic performed because it is presumed to give a longer shelf life to colonche, since it can be stored in this way before the inoculum is added.

DNA Extraction and Sequencing

Genomic DNA was extracted for all the samples with the ZR Soil Microbe DNA MiniPrep kit (Zymo Research) followingthe manufacturer's protocol. DNA was quantified using Qubit Fluorometric Quantitation (Thermo Fisher Scientific) and its quality was assessed on a 1% agarose gel. The obtained high-quality DNA samples were stored at -20°C util the library preparation. The libraries and targeted metagenomic sequencing were performed at ZymmoBIOMICS Service (Irvine, CA). Libraries of 16S rDNA and ITS amplicons were sequenced on the Illumina® MiSeq™ platform 2 × 300 bp paired end. For bacteria, the V3-V4 regions of the 16S rRNA were amplified as has been reported in previous works (Caporaso et al., 2011; Li and Yue, 2016). For fungi, the internal transcribed spacer (ITS) was amplified using the ITS2 primers (Yao et al., 2010; Badotti et al., 2017; Baldrian et al., 2021).

Microbiome Analysis in the Colonche Samples

The 16S rRNA and ITS amplicon sequences were processed using QIIME 2™ (Caporaso et al., 2010; Bolyen et al., 2019), version qiime2-2018.8. For all data, the DADA2 (Callahan et al., 2016) pipeline was used for quality filtering, removal of chimeric sequences, merge paired end reads and generate a table of amplicon sequence variants of each dataset (ASVs, Callahan et al., 2017). To eliminate the bases corresponding to the primers, the first 16 bases of the forward reads and 24 bases of the reverse reads of the 16S rRNA sequences were trimmed. From the ITS sequences, 22 and 24 bases of forward and reverse reads were clipped, respectively. Furthermore, to remove low-quality regions of the sequences, each read was clipped to some position where the quality decreases and was determined with the interactive quality plots of QIIME 2™ (Bolyen et al., 2019). The 16SrRNA sequences were truncated to 315 bases for forward reads and 250 bases for reverse reads, and the ITS sequences were truncated to 310 bases and 215 bases for forward and reverse reads, respectively.

Taxonomy was assigned to the representative unique sequences from each ASVs based on the Naïve Bayes classifier (Bokulich et al., 2018) and annotated according to the Greengenes 13_8 database (DeSantis et al., 2006); for the 16S rRNA data and from the ITS data the UNITE databasev8.0 (Nilsson et al., 2019) was used. For each dataset, the ASVs represented by less than 10 sequences were removed in all samples, and the ASVs that were classified as plant chloroplast, mitochondria, archaea, unassigned sequences, or only assigned to *phylum* level were also eliminated. For diversity and statistical analysis, the ASVs tables of bacteria and fungi were normalized by their relative abundance (Fitzpatrick et al., 2018; Solís-García et al., 2021).

Diversity and Statistical Data Analysis

Alpha diversity was evaluated with the Hill numbers (${}^{q}D$), where the order q determines the sensitivity of the measure to therelative abundance (Chao and Chiu, 2016). ${}^{0}D$ is equivalent to therichness; the measure ${}^{1}D$ counts the ASVs proportionally to their abundances and corresponds to the effective numbers of common ASVs; the measure for ${}^{2}D$ considers the most abundant ASVs and can be interpreted as the effective number of dominant ASVs (Chao et al., 2014; Montes-Carreto et al., 2021). The comparisons of the diversity measures among colonche management practices were made under the same sample coverage and the no overlap in the 95% CI values indicates significant differences (Cumminget al., 2007). Sample coverage values, ${}^{q}D$, and their confidence intervals were calculated with the iNEXT R package 3.5.3 (Hsieh et al., 2016), using as an endpoint the maximum number of sequences in each treatment.

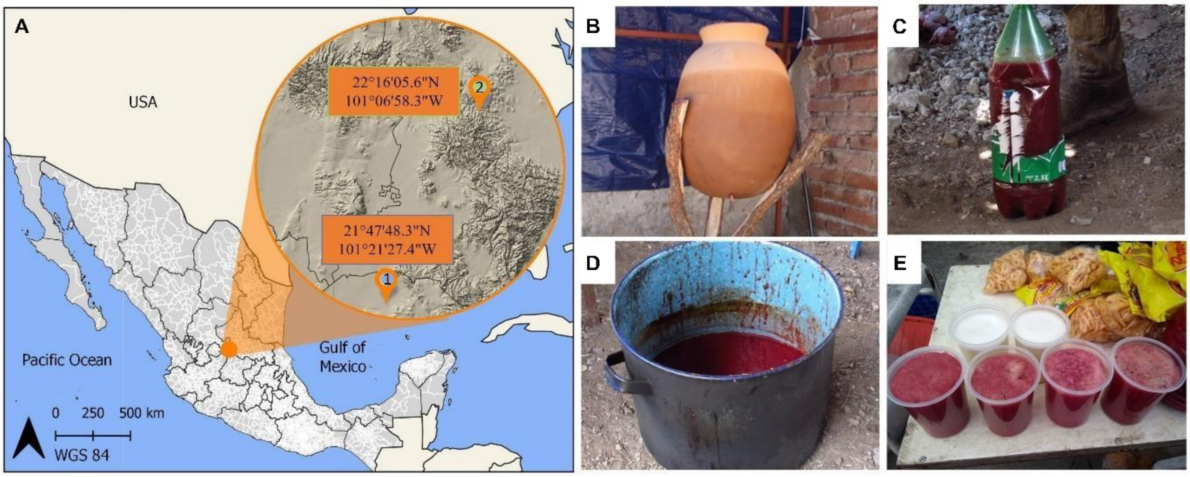

FIGURE 1 | Sampling sites and colonche samples (A1) the locality of Laguna de Guadalupe in Guanajuato state; (A2), Mexquitic de Carmona in San Luis Potosí. (B) Claypots where spontaneous fermentation occurs; (C) Inoculum stored from the last season; (D) Cooked and boiled Cactus prickly pear fruits where sugars are concentrated; (E) Inoculated samples ready to sell in the local markets.

For beta diversity analyses, each phylogenetic tree was constructed with the ASVs of bacteria or fungi of theinoculated and spontaneous colonche management practices. The sequences alignment was made with MAFFT, the trees wereinferred with FastTree and then rooted at its midpoint. TheASVs tables of bacteria and fungi log2-transformed and thedissimilarity matrices of the Unifrac weighted and unweighted distances were calculated with the phyloseq (McMurdie andHolmes, 2013) and vegan packages (Oksanen et al., 2013). The phylogenetic dissimilarities of the bacterial and fungal communities were represented with the ordination method of non-metric multidimensional scaling (NMDS) based on the Unifrac weighted and unweighted distances (Lozupone et al., 2011). To compare the structure of each community of the inoculated and spontaneous colonche management practices a permutational multivariate analysis of variance (PERMANOVA)was computed using the vegan package with 999 permutations.

Significant differences in the relative abundance of each taxon between the inoculated and spontaneous colonche management practices were evaluated through the Mann-Whitney-Wilcoxon test with an FDR correction in R v.3.5.2 software, considering as a significant values $P < 0.05$. The shared bacteria and fungi ASVs among both treatments were plotted as a Venn diagram with the VennDiagram package (Chen and Boutros, 2011).

RESULTS

Preprocessing and Taxonomic Classification

To visualize the changes in the bacterial communities between fermentation management practices we obtained pair-end sequencing of the V3-V4 region of the 16SrRNA leads to a total of 2,398,545 reads, with an average of 28,769.79 (± 33,516.46) reads per sampling, then, after filtering the ASVs table, a total of 701 in all 16S samples, belonging to 173 bacterial genera (**Supplementary Table 1**). For fungal communities by ITS sequence, a total of 1,505,383 pair-end were obtained with an average of 62,724.291 (± 23,303.49) reads for all the sampling which composed a total of 203 ASVs; then, after filtering the table with 0.01% of relative abundance, 201 ASVs were obtained, belonging to 187 yeast genera (**Supplementary Table 1**). The bacterial and fungal communities of each colonche management practices had a sample coverage of 100% suggesting that the most of the ASVs were captured (**Supplementary Figure 1A**). Also, rarefaction curves for all the samples reached the plateau indicating that the sequencing depth was sufficient to covermost of the bacterial and fungal diversity in each colonche management practices (**Supplementary Figure 1B**).

Colonche Microbiome Is Partially Consistent With the Management Hypothesis

To analyze our hypothesis, the alpha diversity was estimated using the Hill numbers (^{q}D). For the ASVs of the bacterial community (**Supplementary Table 2**), the clay pots samples showed a higher richness ($^{0}D = 543 \pm 0.121$), followed by the spontaneous samples ($^{0}D = 136 \pm 0.433$), the inoculated samples($^{0}D = 128 \pm 0.929$), the cooked samples ($^{0}D = 113.00 \pm 3.485$), and being the inoculum samples ($^{0}D = 47 \pm 0.163$) the ones withthe lowest richness (**Figure 2A**). Also, the clay pot samples werethe most diverse ($^{1}D = 131.575 \pm 1.412$; $^{2}D = 38.087 \pm 1.212$) compared with the other colonche management practices(**Figures 2B,C** and **Supplementary Table 2**). The diversityvalues of the effective number of common and dominant ASVs were significantly higher in the inoculated samples ($^{1}D = 18.277 \pm 0.929$, $^{2}D = 11.507 \pm 0.04$) contrarily to the spontaneous samples ($^{1}D = 11.081 \pm 0.049$, $^{2}D = 4.33 \pm 0.019$; **Figures 2B,C**). Thus, there is a reduction in richness from

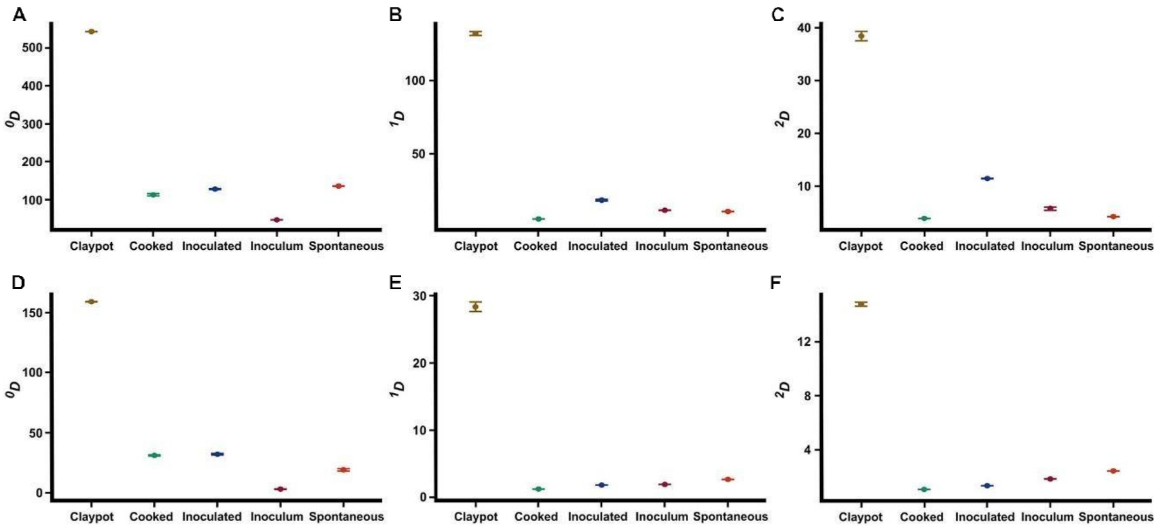

FIGURE 2 | Comparison of the richness and alpha diversity of the bacterial (A–C) and fungal communities (D–F) between the different colonche management practices estimated with the Hill numbers (^qD). Interval plots of richness (A,D), effective number of common amplicon sequence variants (ASVs) (B,E), and effective number of dominant ASVs.

spontaneous to inoculated fermentation practices in the colonche microbiome, which is consistent with our hypothesis. The richness of the ASVs of the fungal community (**Figure 2D**and **Supplementary Table 2**) showed a different pattern, the clay pots also display the highest values (^0D = 159 ± 0.151), followed by the inoculated samples (^0D = 32 ± 0.539), then the cooked samples (^0D = 31 ± 0.458), the spontaneous samples (^0D = 19 ± 0.917), and finally the inoculum with the less richness (^0D = 3 ± 0.151). Diversity of clay pots samples (^1D = 28.873 ± 0.214, ^2D = 14.787 ± 0.145) was higher than that of the other colonche management practices (**Figures 2E,F**). In contrast, diversity of common and dominant fungal ASVs was significantly higher in the spontaneous samples (^1D = 2.667 ± 0.004, ^2D = 2.442 ± 0.004) than in the inoculated samples (^1D = 1.826 ± 0.007, ^2D = 1.346 ± 0.004; **Figures 2E,F**).

Colonche Microbial Differences Between Spontaneous and Inoculated Fermentation Practices

To characterize the differences between spontaneous and inoculated colonche microbiome, the beta diversity of bacterial and fungal communities was represented with a NMDS using weighted and unweighted Unifrac distances (**Figure 3** and **Supplementary Figure 2**). Although phylogeneticdissimilarities between the bacterial groups in spontaneous and inoculated fermentations by the unweighted Unifrac distance allow visualizing the splitting of both bacterial communities($p < 0.036$), there is an inoculated sample that is closer tothe spontaneous samples, and the spontaneous fermentedsamples are more disperse and less clustered (**Figure 3A** and **Supplementary Table 3**). The weighted Unifrac distances partially allow discriminating fungal community ($p < 0.047$),it can be seen that the spontaneous bacterial communities are clustered, while the inoculated samples are more variable and there are samples that overlap with the spontaneous treatment (**Figure 3B** and **Supplementary Table 4**). Both results are supported by PERMANOVA analysis (999 permutations). Summarizing, the overlap in microbial communities for both types of fermentation practices might reflect a common shared composition of microorganisms occurring in the *Opuntia streptacantha* substrate. The variation in the spontaneousbacterial community is consistent with the data of alpha diversity, while for fungal communities there are less differences among treatments, which might reflect the high abundance and dominance of *Saccharomyces* genus, as referred to for alpha diversity (**Figure 2B**).

Colonche Microbial Genus Composition in the Different Fermentation Practices

The Microbial Community in Spontaneous Fermentation: Clay Pots and Spontaneous Colonche

Besides different diversity levels, we found that clay pots have a high richness in the composition of bacteria and fungi at the genus level (**Figure 2**). Among the most abundant bacteria genera occurring in the clay pots are: *Arthrobacter* (14.92%), *Elstera* (10.12%), *Alkanindiges* (7.72%), *Massilia* (6.92%), *Pseudomonas* (5.18%), *Nocardioides* (1.79%), *Roseomonas* (1.62%), *Rhizobium* (1.40%), *Blastococcus* (1.39%), *Achromobacter* (1.20%), *Brevundimonas* (1.15%). While for fungal community, *Penicillium* (38.15%), *Cladosporium* (9.70%), *Didymella* (9.60%), *Wickerhamomyces* (8.90%), *Naganishia*, (7.86%), *Alternaria* (6.42%), *Rhodotorula* (4.06%), *Fusarium* (3.02%), *Saitozyma* (1.62%), *Aureobasidium* (1.38%), *Vishniacozyma* (1.14%), *Cystofilobasidium* (1.01%) and although *Saccharomyces* (0.42%) ends up as the most dominant yeast in the spontaneous fermentation, its abundance is lower in the clay pots (**Figure 4**).

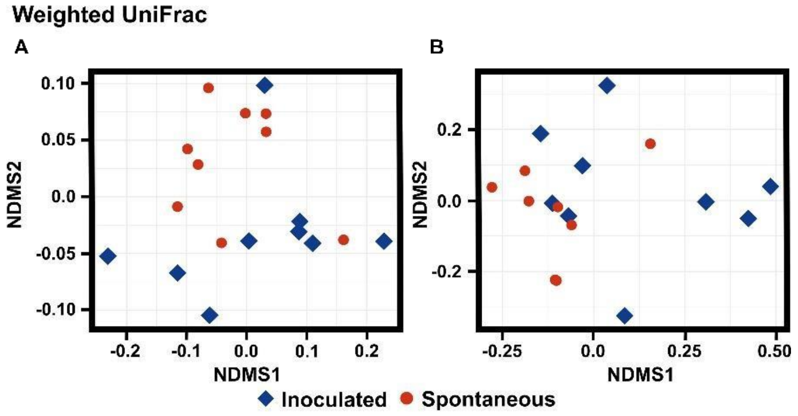

FIGURE 3 | Non-metric multidimensional scaling (NMDS) plots-based (A) on UniFrac weighted distance of the bacterial community structure; (B) an Unifrac weighted distances of the fungal community structure associated with inoculated and spontaneous fermentation practices in the colonche production.

At the end of the spontaneous fermentation process, 10 fungal ASVs (*Aureobasidium*, *Candida*, *Cladosporium*, *Pichia*, *Saccharomyces*, *Torulaspora*, *Rhodotorula*, *Wickerhamomyces*, one unidentified taxon and one not assigned fungal) are shared within the clay pots. This group is mainly involved in the final stages of the fermentation process of the spontaneous fermentation. Four groups are exclusive of the spontaneous fermented colonche (*Dekkera*, *Kazachstania*, *Kluyveromyces* and *Knufia*) and 45 are unique for clay pots. This behavior is similar in the bacterial community, in which 6 genera (*Massilia*, *Elizabethkingia*, *Clostridium*, *Bacillus*, *Alkanindiges* and one not assigned taxon) are shared with the spontaneous final product and the clay pots. For instance, 12 genera (*Weissella*, *Tanticharoenia*, *Tatumella*, *Streptococcus*, *Rheinheimera*, *Pediococcus*, *Lactococcus*, *Lactobacillus*, *Gluconacetobacter*, *Faecalibacterium*, *Dorea* and *Aeromonas*) are present in thefinal product of spontaneous fermentation, being particularly remarkable *Lactobacillus* and *Leuconostoc*, which are present in higher abundance (**Figure 4**). Finally, 71 ASVs are exclusive of the microbiota communities of the clay pots.

The Microbial Community in the Inoculated Fermentation: Inoculums, Cooked and Inoculated Colonche

It can be visualized that the inoculums are the samples with the lowest richness of bacteria and yeasts; for instance, we identified only 7 bacteria and 2 yeast genera, mainly dominated by multiple taxa of Lactic Acid Bacteria (LAB) as: *Lactobacillus* (24.60%), *Leuconostoc* (10.34%), *Alkanindiges* (8.65%), *Pediococus* (6.92%), while yeasts are dominated by *Saccharomyces* (99.9%) and *Kazachstania* (0.01%). Surprisingly, there were a higher number of ASVs for the cooked samples with 32 bacteria genera (**Supplementary Table 5**) and 21 yeasts, contrasting with the final product of the inoculated fermentation, which had fewer ASVs (**Supplementary Table 6**).

As mentioned above, in the inoculated fermentation process all microbial ASVs of the inoculums are shared with the inoculated final product. Also, *Alkanindiges*, *Clostridium* *Corynebacterium*, *Gluconacetobacter*, *Lactobacillus*, *Leuconostoc*, *Massilia*, *Pediococcus*, *Sphingomonas*, *Staphylococcus*, *Weissella* and one not assigned taxon are shared between the cooked and the inoculated samples. *Dorea* and *Elstera* are the onlytwo exclusive genera of the inoculated samples and 18 genera (*Actinomycetospora*, *Actinotelluria*, *Albidovulum*, *Arthrobacter*, *Blastococcus*, *Dietzia*, *Gaiella*, *Helcobacillus*, *Micrococcus*, *Microlunatus*, *Nocardioides*, *Oceaniovalibus*, *Ochrobactrum*, *Roseomonas*, *Solirubrobacter*, *Sporosarcina*, *Streptomyces* and *Tanticharoenia*) are exclusive of the cooked samples.

For the fungal community we registered 9 genera being commonly shared between the cooked treatment and inoculated samples (*Candida*, *Cladosporium*, *Dipodascus*, *Hanseniaspora*, *Kazachstania*, *Kluyveromyces*, *Saccharomyces*, *Torulaspora* and one unidentified taxon). The genera *Alternaria*, *Arthrinium*, *Cryptococcus*, *Didymella*, *Filobasidium*, *Fusarium*, *Mucor*, *Naganishia*, *Rhodotorula* and *Starmerella* are exclusiveof cooked samples and only *Aureobasidium*, *Dekkera*, *Issatchenkia* and *Pichia* are unique for the final product of inoculated fermentation.

The Microbial Composition Between Spontaneous and Inoculated Fermentations

For bacterial communities we found that 12 ASVs are shared among the fermentation practices, like *Lactobacillus* ($p < 1e-1$), *Alkanindiges*, *Clostridium*, *Dorea*, *Faecalibacterium*, *Gluconacetobacter*, *Lactococcus*, *Leuconostoc* ($p < 1e-1$), *Pediococcus* ($p < 1e-1$), *Tatumella*, *Tanticharoenia*, and *Weisella* ($p < 1e-1$). For instance, 6 genera are exclusive to spontaneous treatment like *Aeromonas*, *Bacillus*, *Elizabethkingia*, *Massilia*, *Rheinheimera* and *Streptococcus* and 4 are exclusive of the inoculated samples (*Staphylococcus*, *Sphingomona*, *Corynebacterium*, *Elstera*) (**Figure 5A**). In the fungal communities, we identified 11 genera shared among samples under different fermentation practices: *Aureobasidium*, *Candida*, *Cladosporium*, *Dekkera* ($p < 1e-1$), *Hanseniaspora*, *Kazachstania* ($p < 1e-6$), *Kluyveromyces*, *Pichia*, *Saccharomyces*, *Torulaspora* and other unidentified taxa. The inoculated samples displayed

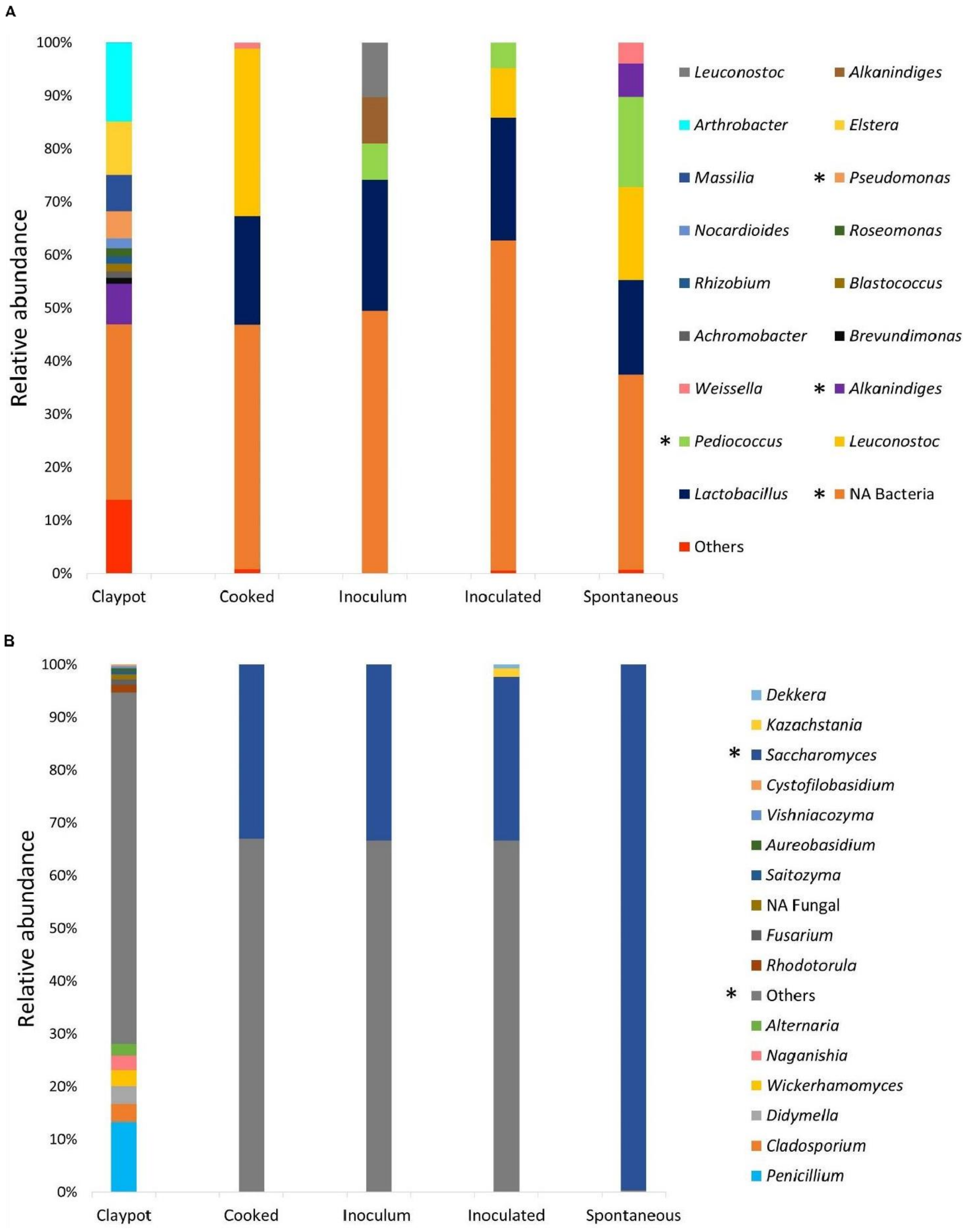

FIGURE 4 | Composition of the (A) Bacterial Genera composition of the community associated with the management practices and colonche production stages and, (B) the fungal Genera composition. Low abundance taxonomic groups (relative abundance < 1%) were reported as others. NA mean not assigned. The asterisk indicates significant differences in taxa relative abundance between management practices.

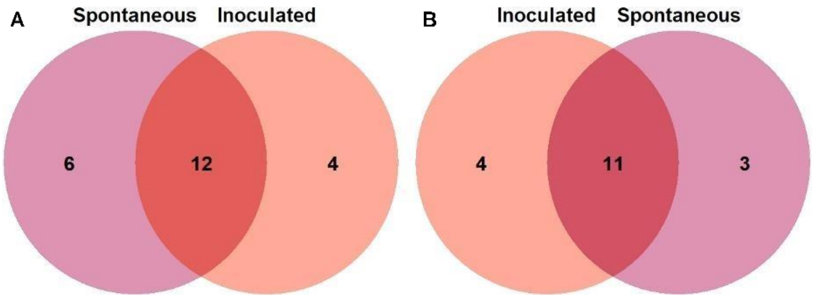

FIGURE 5 | Venn diagrams of the number of unique and shared amplicon sequence variants (ASVs) of the (A) bacterial and (B) fungal community associated with the fermentation practices of colonche samples inoculated (red) and spontaneous (purple).

4 exclusive ASVs (*Wickerhamiella*, *Issatchenkia*, *Dipodascus* and *Clavispora*), while the spontaneous fermentation samples registered 3 unique ASVs (*Wickerhamomyces*, *Knufia* and one not assigned genus) (**Figure 5B**).

DISCUSSION

Differences Between Spontaneous vs. Inoculated Fermentations

Our results confirm that spontaneous and inoculated fermentation practices significantly differ in the composition of microbial assemblages and the relative abundance of bacterial and fungal taxa in fermenting communities. These results are in concordance with most of the literature reporting that spontaneous fermentations exhibit a higher number of microbial species than inoculated products (Tamang et al., 1988; Raspor et al., 2002; Haruta et al., 2006; Domizio et al., 2007; Alves et al., 2010; Hong et al., 2015; Anagnostopoulos et al., 2020; Lu et al., 2021). These results confirm the reduction of diversity hypothesis, as can be visualized in **Figure 2**, where the lowest values of diversity for both bacteria and fungi were recorded in the inoculums and the reduction at the final compositionfor bacterial communities occurs in the inoculated samples. Nevertheless, this relation is not unidirectional for fungi, for which we observed small differences, contrarily to what has been previously reported (Raspor et al., 2002).

Fermentation traditionally occurs spontaneously andis initiated by a diverse community of indigenous yeastsand bacteria associated to the plants, the environment, orthe fermentation facilities where it is produced (Pretoriuset al., 1999; Motarjemi, 2002; Bokulich et al., 2013; Bokulich and Mills, 2013; da Silva Vale et al., 2021). In different traditional fermented beverages, the yeast genera *Hanseniaspora*, *Pichia*, *Metschnikowia*, *Candida*, *Torulaspora*, *Rhodotorula*, *Cryptococcus*, *Lachancea*, *Zygosaccharomyces* have been recorded as the most common at the initial stages of the successional process of fermentation, while strains of *Saccharomyces cerevisiae* become dominant at the last stages (Krieger-Weber et al., 2020). Although successional dynamics were not assessed in our current analysis, it could be considered that the fermentative environment as the clay pots where spontaneous fermentation occurs and the cooked samples before the inoculation, displayed a higher richness at both initial stages. This information also confirms that there is a marked dominance of the genus *Saccharomyces* at the final stages of the fermentation, and it occurs independently if it is spontaneous or inoculated fermented colonche. This can be explained because of the *Saccharomyces* capacity to quickly adapt to variable environmental conditions (Legras et al., 2018).

Our results confirm that the non-*Saccharomyces* yeastgroup comprises a variety of oxidative, weakly fermentative and strongly fermentative yeasts of genera like *Rhodotorula*, *Cryptococcus*, *Hanseniaspora*, *Candida*, *Pichia*, *Issatchenkia*, *Metschnikowia*, *Lachancea*, *Zygosaccharomyces*, *Starmerella*, *Torulaspora* and others (Barata et al., 2012), which are found at different frequencies at the clay pots and the cooked samples. This group has low fermentation power and are sensitive toprevailing anoxic conditions and increasing ethanol levels (Martinez et al., 2013; Quirós et al., 2014; Morales et al., 2015). Depending on the fermentative capacity and metabolic activity of the individual species, non-*Saccharomyces* yeasts are able to maintain their viability until the middle of fermentation before starting to decline (Xufre et al., 2006; Renouf et al., 2007;Andorrà et al., 2008; Zott et al., 2008, 2010; Bagheri et al., 2015;Sha et al., 2017). Nevertheless, the current results showed the dominance of *Saccharomyces* over the non-*Saccharomyces* groups in the final products of both types of fermentations. A similar observation was reported for other fermented beverages around the world (Tamang et al., 1988; Lyu et al., 2013; Yang et al., 2016; Sha et al., 2017).

In both types of fermentation, we identified constantly the *Pediococcus* genus. Some species of this genus are associated with spoilage of fermented beverages, especially beers and wines (Mokoena, 2017). It has been associated with the synthesis of excessive diacetyl, exopolysaccharides, and biogenic amines, all of which have a detrimental impact on the quality of the product (Wade et al., 2019). However, recent research has supported the contention that *Pediococcus* spp. can grow in wines considered to be microbiologically stable. In fact, the presence of *Pediococcus* spp. in wines not always lead to spoilage, and new findings have suggested potential uses for *Pediococcus* spp.to contribute to desirable characteristics of wines under certain circumstances. As *Pediococcus* was one of the most common genera identified in colonche samples, further studies through High-performance liquid chromatography (HPLC) should be addressed to characterize if the high abundance is associated with the spoilage or if it brings desirable characteristics to colonche and the distinction in the aromatic profile between fermentation practices.

The presence of yeast genera like *Wickerhamiella*, *Clavispora*, *Dipodascus* and *Issatchenkia*, has been described previously in pulque fermentation (Rocha-Arriaga et al., 2020). For instance, the differences of the fungal community between the inoculated fermentation are due to the common use of pulque to improve their fermentation or the use of the same containers for pulque production. *Torulaspora* is one of the few microorganisms previously identified in colonche samples (Ulloa and Herrera, 1978). By the current sampling we identified its presence in clay pots and in the cooked samples, which might represent the initial stages of fermentation. However, at the end of the fermentation under both types of practices low numbers of this genus were identified, and such low population density may be due to strict anaerobic conditions and low invertase activity (Visser et al., 1990; Hanl et al., 2005), mainly promoted by *Saccharomyces* species.

Kluyveromyces was also found in the colonche samples, it is a genus that has been isolated from a great varietyof habitats and has been described to have high metabolic diversity and a substantial degree of intraspecific polymorphism. Therefore, several different biotechnological applications have been investigated with this yeast: production of enzymes, single-cell protein, aromatic compounds, and other applications (Varela et al., 2017). However, it cannot grow under strictly anaerobic conditions and the ethanol production is almost exclusively linked to oxygen limitation (Visser et al., 1990; van Dijken et al., 1993; Bellaver et al., 2004). In this sense, the higher abundance of *Kluyveromyces* genus in cooked and inoculated colonche samples might be due to a low alcohol content, but further studies are still needed to address the relationship between physicochemical attributes and the presence of microbial communities.

Kazachstania genus is typically encountered in the plant substrate, for instance, it is associated with grapevines and, in a low frequency, in grape must. Although it has not yetbeen characterized in cactus prickly pear fruits, this yeast genus provides positive aroma attributes that should be explored further. Its low presence in the final inoculated colonche productmight be due to the dominance of the *Saccharomyces* which display a higher abundance in this treatment. *Rhodotorula* isalso a common basidiomycete yeast that has been reported in several dairy products, it has a weak fermentative capacity, and has also been found associated with insects as vectors (Fonseca and Inácio, 2006; Kemler et al., 2017). The presence of this basidiomycete yeast might reflect the presence of insects closer to the clay pots and the low cautions in the storage of the cooked substrate. Nevertheless, this yeast wasnot found at the end of fermentation under both treatments, suggesting that hygienic practices are performed or inhibited during fermentation. In general, fungi held more stable ranges of diversity indexes in most of the samples analyzed, a similar pattern previously reported in beverages like pulque (Rocha-Arriaga et al., 2020).

Multiple strains of LAB from the *Lactobacillus* genus were registered in this study, *Lactobacillus* was the most abundant genus of bacteria, found abundantly (∼ 50%) in all phases of colonche fermentation except in clay pots. LAB are found in decomposing plant material and fruits, in dairy products, fermented meat and fish, cereals, beets, pickled vegetables, sourdough, silages, fermented beverages, juices, sewage and in cavities of humans and animals (König et al., 2009; Devi et al., 2013; Liu et al., 2014; Mokoena, 2017). LAB genera include *Lactobacillus, Lactococcus, Leuconostoc, Pediococcus, Streptococcus, Aerococcus, Alloiococcus, Carnobacterium, Dolosigranulum, Enterococcus, Oenococcus, Tetragenococcus, Vagococcus* and *Weissella* (Khalid, 2011), with *Lactobacillus* being the largest genus, including more than 100 species that are abundant in carbohydrate-rich substances and most of them are the most common and shared among samples of colonche in both fermentations process. It has been characterized that some LAB are used as probiotics, due to their health benefits (Ljungh and Wadstrom, 2006; De Leblanc et al., 2007; Azaïs-Braesco et al., 2010; Evivie et al., 2017). Although the main aim of this work was not to identify possible probiotics of LAB genera in colonche, we suggest that further studies in this direction may contribute to improve intestinal microbiota and human health through this beverage.

Our current study identified that 12 bacterial and 11 fungal ASVs are shared between spontaneous and inoculated colonche samples. Nevertheless, only the bacterial genera *Lactobacillus*, *Leuconostoc*, and *Pediococcus* and the *Saccharomyces* yeasts were the most abundant for both fermentation practices and appear in the inoculum and in the cooked samples. We propose as a first exploratory analysis that these 4 genera might reflectthe microbial core of colonche because they appear commonand abundantly in all the colonche samples. These genera are common throughout the fermentation of several fermented beverages and are closely related to food quality (Zhu et al., 2020;An et al., 2021; Ban et al., 2022). Nevertheless, further analysis as functional assignation and metaproteomics under a network approach can give insights of the functional microorganism’s core and the relevance to achieve a predictable product.

The Clay Pots: Not a Starter Culture but a Practical Reservoir for Future Fermentations

The clay pots displayed some microorganism’s genera associated with pathogenic activity, as are the cases of some strainsof *Clostridium*, *Pseudomonas*, and some species of the genus *Pediococcus*. Nevertheless, through the fermentation stages these pathogenic strains disappear, perhaps because of the multiple strains of *Lactobacillus* in the spontaneous fermentation process. LAB have been applied in food preservation, partly due to their antimicrobial properties and because their capabilityto acidify the environment, making it harmless for other bacterial groups (Cizeikiene et al., 2013; Arena et al., 2018; Singh, 2018). Bacteriocins are a group of potent antimicrobial peptides produced by some microorganisms including LAB, primarily active against closely related organisms, mostly Gram-positive bacteria to gain competitive advantage for nutrients

(Parada et al., 2007; Zacharof and Lovitt, 2012; Mokoena, 2017; Timothy et al., 2021). In fermented foods, LAB display various antimicrobial activities, through production of various metabolites, including lactic acid, hydrogen peroxide, and bacteriocins. Therefore, the high presence of *Lactobacillus* might reflect the drastic changes in the composition from the clay pot samples through the final product, thus inhibiting the pathogens in the environment.

As mentioned above, clay pots displayed the highest richness of bacterial and fungal genera, including several non-*Saccharomyces* genera, some beneficial bacterial groups as LAB and some detrimental bacterial groups associated with the spoilage of the beverage. Nevertheless, some of these microorganisms contribute to subsequent microbial growth and brings a stable community, for instance, 10 fungal ASVs and 6 bacterial genera are shared between the clay pots and the spontaneous colonche. In this sense, a stable consortium as an inoculum might not be required in spontaneous fermentation due to the presence of microbial diversity in the clay pots that can promote a starter community for fermentation process. Further studies should consider including other microbial inputs, for example the cactus pear fruits that are exposed to a variety of microorganisms derived from the environment (e.g., surfaces and soil), producer's hands, and tools that can contribute to microbial communities and the quality of colonche as has been performed with cocoa fermentation (Schwan and Wheals, 2004; Lefeber et al., 2010; Figueroa-Hernández et al., 2019; Viesser et al., 2021), in which these factors contribute to the quality of the product.

The production of spontaneous colonche is mostly performed in clay pots, nevertheless, sometimes producers store the peeled cactus prickly pear fruits in plastic containers and then the fruits are placed inside the clay pots (Ojeda-Linares et al., 2020). Although we did not characterize the microbial and the physicochemical differences between the containers, it has been recorded that the material of the fermentation containers plays a significant role changing the abundance of specific genus as *Lactococcus* and *Pedioccous* and can affect pH values favoring a quicker fermentation (Liu et al., 2019). It is possible that the presence of these genera is favored by a previous storage in plastic containers and changes in the pH values might also change the dynamic in the clay pot by acidifying the medium. Though, further analysis should be performed to characterize the effect of the containers for colonche production.

The Inoculums: Insights for Unconscious Microorganisms' Selection

The producers of traditional fermented beverages select inoculums as a practical way to acquire an optimal fermentation capacity and their capability to give consistent quality and aroma compositions through the fermentation process. As documented before, the selection of inoculums is related to a community of bacteria and yeasts that improves the fermentation dynamicsand is mainly characterized by a reduction of diversity (Alveset al., 2010; Anagnostopoulos et al., 2020; Lu et al., 2021). Inthe colonche production, *cinaiste* is the common name of the inoculum, it is stored from previous batches year after year, and our data indicate a marked dominance of *S. cerevisiae* strains and a higher number of reads compared with the restof samples analyzed. The large inoculum of active *S. cerevisiae* cells in most cases ensures a rapid dominance of a single strain and will therefore likely reduce any impact that the natural microbiota may have if spontaneous fermentation is allowed.In addition, the inoculum shows the lowest bacterial diversity, which is consistent with a reduced richness in starter cultures, a pattern that has been previously documented for the selectionof starter cultures in other traditional fermented products (Orjiet al., 2003; Zorba et al., 2003; Freire et al., 2015; Fagbemigunet al., 2021; Lima et al., 2021). Our results therefore expand the documentation of the deliberate selection of microbial consortia to acquire an optimal fermented product.

Selection of microorganisms is an attempt to enhance a fermentative environment, such type of efforts to transform the environment are proposed to play an important and underappreciated role in shaping biotic communities and evolutionary processes (Jones et al., 1997; Odling-Smee et al., 2003; Anderson, 2005). In this context, the studiesof management of microenvironments can make relevant contributions to analyze general processes of domestication of organisms and their environments. Morphological and physiological changes in plants and animals show evidence of domestication and provide insights of the specific human practices that produce them. Analogous changes in microorganisms are not easy to identify. In microorganisms as yeasts, features like the overexpression of metabolic routes like maltotriose and lactate, the loss of sexual reproduction and the decreasing survival in nature, have been considered significant traits to analyze domestication (Gibbons and Rinker, 2015; Gallone et al., 2016; Gibbons, 2019), but there is still a long way to explore in this direction. However, the characterization of the practices performed to produce colonche, particularly the selection of inoculums and their specific consortia, provide a signature of deliberate human management and shaping of the fermenting microenvironments.

Summarizing, our results confirm that the choice of fermentation practice and management practices as cooking the fruits or storing batches year after year influence the composition, structure, and dynamics of microbiota communities inthe different stages of colonche fermentation. Coexistenceof the different fermentation practices and management techniques favors the context to maintain and diversify microbial communities involved in the colonche production. As well, through the carefully reproduction of inoculums, producers promote and direct selection over microbial communities to guide the process of fermentation. The clay pots are important reservoirs of diversity, but they are not commonly considered relevant in fermentation studies. Although the most dominant bacterial and fungal ASVs were not dominant in the clay pot, its presence might highlight the importance at the beginning of the fermentation and the practices performed to clean it are also relevant to maintain the microbial community. Finally, characterizing the management practices that the producers perform to obtain specific traditional products gives insightsabout the knowledge that humans have to reshape biotic communities and micro-landscapes to obtain a quality product at the end of both fermentation types. Thus, it is relevant to conserve these techniques of micro-biocultural heritage, ensure its maintenance and, in some contexts, recover it in the context of the foodscape diversity (Mintz and Du Bois, 2002; Alexiades, 2003, 2009; Marshall and Mejia, 2011; Rocha et al., 2015).

CONCLUSION

The characterization of the microbial communities related to the production of a traditional fermented beverage prepared with fruits of *O. streptacantha* under spontaneous and inoculated fermentation practices, confirmed that the fermentation practices affect the species richness, diversity, and the community structure through spontaneous and inoculated fermentation practices. However, differences are slightly significant for the final products for fungal and bacterial communities, which mightbe the result of the increasing relative abundance of LAB andthe outstanding abundance of *Saccharomyces* genus in final products of both fermentation types. The current information corroborates that there is a continuous selection on microbial communities through the elaboration and management of inoculums. This practice reduces the microbial community and, in the case studied, traditional fermenters select mostly LAB and *Saccharomyces* genera to begin their new batches of colonche year after year. Diverse microorganisms live in the container where fermentation occurs, nevertheless, trough the fermentation dynamics the diversity changes, and a stable community is reached. Although the current research was not directed to assess the differences in the colonche quality, the microbialcomposition at the end of the fermentation and the demandof the consumers for this product supports that both types of fermentation practices yield a good product. However, further analysis as the characterization of microbial functionalities and the physicochemical attributes might help to improve the fermentation practices. Altogether, these results provide the potential of the traditional knowledge and management over microorganisms to produce fermented beverages, thus, the importance to maintain these products, the practices and the diversity associated over the fermentation process. These results are relevant to ensure food security and safety in localities wherefood availability is constrained.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://www.ncbi.nlm.nih.gov/, PRJNA781103.

AUTHOR CONTRIBUTIONS

CO-L conceived, designed, conducted, collected data, and wrote the manuscript. IS-G contributed to analyze the data, constructed figures, and drafted the manuscript. AC conceived, designed, advised, funded, drafted, and reviewed all versions of the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.821268/full#supplementary-material

Supplementary Figure 1 | Rarefaction curves of the sample coverage for (A) bacterial and, (B) fungal community. Rarefaction curves of the observed ASVs of the (C) bacterial and (D) fungal community associated with the colonche stages and fermentation practices.

Supplementary Figure 2 | Non-metric multidimensional scaling (NMDS) plots-based (A) on UniFrac unweighted distance of the bacterial community structure; (B) and the fungal community structure associated with inoculated and spontaneous fermentation practices in the colonche production.

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Discusión general y perspectivas

Conocimiento tradicional: tensiones entre el proyecto hegemónico alimenticio moderno y las memorias del paladar

La cultura dietética y alimentaria ha evolucionado como resultado del conocimiento tradicional y las experiencias de generaciones a lo largo del tiempo. La alimentación se basa en una amplia gama de factores, incluidos el ambiente, la disponibilidad de sustratos comestibles, las propiedades sensoriales, las preferencias étnicas, las creencias o costumbres, las religiones, la socioeconomía, la política regional, las prácticas culturales y las regulaciones dietéticas locales (Tamang *et al.*, 2010). La cultura alimentaria es un proceso dinámico en el tiempo y el espacio, la interacción de distintas culturas, la migración y otros eventos, permiten llevar hábitos alimentarios, las cocinas y rituales de una región a otra ya sea dentro del mismo país o a través de distintos continentes (Tamang *et al*., 2010). Como vimos en el primer capítulo de la presente tesis, en México la elaboración de fermentos se realiza a partir de una amplia gama sustratos de origen vegetal, de los cuales los más importantes son las las plantas con centro de domesticación o diversificación en el país, como el maíz, los agaves y diversas cactáceas. No obstante, también ocurre la incorporación de nuevos sustratos y alimentos en la dieta debido a la migración de diversos grupos humanos ya sea a nivel nacional o un ejemplo claro es la producción del vino de palma introducido por los filipinos, el cual posteriormente sirvió para incorporar nuevas herramientas para diversificar otros productos, como es el caso del mezcal.

Por otro lado, la velocidad de la pérdida, la erosión y la reducción de los conocimientos ecológicos tradicionales son motivo de preocupación a nivel mundial (Ramírez, 2007; Reyes-García *et al*., 2013; Ballick, 2017). En el caso de las bebidas fermentadas, distintos factores amenazan su continuidad, principalmente debido a que estas no son reconocidas comúnmente como parte de estos sistemas de alimentación y en menor grado como conocimiento tradicional (Ramírez, 2007; Reyes-García *et al*., 2013; Nehal, 2013; Counsin *et al*., 2017). Sin duda, un primer factor de riesgo para las bebidas fermentadas tradicionales es no reconocerlos como parte del grupo de conocimiento ecológico tradicional (Nehal, 2013; Altay *et al*., 2013; Tafere, 2015; Kaur *et al*., 2019). No reconocerlos limita darles la relevancia que tienen como base fundamental de los panoramas alimentarios, soslaya la diversidad biocultural asociada, impide generar mecanismos para fomentar su conocimiento y conservación o como una estrategia para darle robustez a la soberanía alimentaria.

A continuación, se señalan algunas amenazas que pueden estar asociadas a los conocimientos ecológicos tradicionales en bebidas fermentadas tradicionales de México: 1) el cambio en las creencias tradicionales, sobre todo en las regiones que se han sido historia de colonizaciones, diferentes estudios han señalado que el conocimiento generacional ha sido erosionado lentamente a medida que la ideología de la modernidad se infiltra en la mente de las generaciones jóvenes (Berkes, 2012; Wavey, 1993; Ellen, 2007; Tang & Gavin, 2016). En este sentido, se ha descrito y observado que la producción de bebidas fermentadas tradicionales en México se ha ido reduciendo en gran medida por una entrada de la constante idea del progreso. Alrededor del mundo se ha registrado el desuso de bebidas fermentadas por diferentes motivos como la facilidad de adquirir otros productos que pueden ser considerados como sustitutos y que además en la concepción colectiva son considerados como productos con un mayor estatus, tal es el caso de las bebidas alcohólicas industriales (cerveza, whisky) y bebidas gasificadas como los refrescos (Ólafsdóttir, 1998; Smith y Solgaard, 2000; Jenatton y Morelaes, 2020). Además, estas bebidas al estar disponibles en anaqueles comerciales no tienen que ser elaboradas de forma doméstica e involucran una menor carga de trabajo. Estas dos características las hemos identificado particular mente en el colonche y son amenazas latentes para su continuidad.

En la actualidad también reconocemos que los cambios en el ambiente y en la accesibilidad a sus recursos son una fuerte amenaza para su continuidad. Esto puede ocurrir por el crecimiento de la población en las localidades, en donde se reducen las áreas de cultivo o las zonas de recolección, en el caso mexicano existe una reducción de las áreas comunes de cultivo en donde esta fragmentación limita el acceso a los recursos. Este caso también lo registramos para a producción del colonche en la comunidad de Laguna de Guadalupe en donde actualmente se está generando una fragmentación de los espacios comunes como es el cerro en donde se realiza la cosecha de tunas. Esto principalmente por la privatización de los ejidos para ser sustituidos con la siembra intensiva de frijol y alfalfa. Asimismo, se han registrado casos asociados a la producción de mezcal en donde el uso excesivo de los recursos y la tensión derivada entre grupos locales y externos han generado conflictos respecto al uso de estos agaves (Vanguardia mx, 2021; Aristegui noticias, 2021; Suracapulco, 2021). Recientes trabajos periodísticos han registrado que en algunas localidades mezcaleras en el estado de Guerrero los productores tradicionales de mezcal han sido desplazados por el narcotráfico, esto debido a que los narcotraficantes decidieron apropiarse de los espacios y tierras para la producción del mezcal. Este fenómeno ocurre debido a que las ventas de mezcal generan un mejor rendimiento económico y a comparación con la siembra y venta de amapola, la venta del mezcal tiene un buen mercado. Así, grupos armados han desplazado y se han apoderado de una comunidad entera de productores de mezcal (Vanguardia mx, 2022; Sur acapulco, 2022). Básicamente en todas partes del mundo, el crimen, la guerra y el militarismo han afectado gravemente a los pueblos indígenas y a pequeñas localidades, particularmente al hacerse con el control de los recursos naturales sin compensación ni pago (Trask, 2009).

Así mismo, esta ruptura entre la relación entre los seres humanos y su ambiente en donde crecieron o trabajan genera cambios en la forma de interactuar con sus sistemas ecológicos, provocando así la pérdida en los modos de transmisión de estos conocimientos. La pérdida de estos métodos de transmisión es clave ya que ha sido caracterizado como una de las formas directas para la erosión de estos conocimientos (Derman, 2003; Jhons y Sthapit, 2004; Srithi *et al*., 2009; Benyei Peco *et al.*, 2020). Por ejemplo, la migración de grupos culturales y principalmente la de los jóvenes a otros lugares en busca de mejores oportunidades o desplazados por algún tipo de violencia, también representa un riesgo debido a que se pierde el interés en la tradición, la cultura y el declive en el conocimiento tradicional comienza gradualmente a través del desinterés o la baja conexión con su ambiente (Lizarralde, 2001; Case *et al*., 2005; Reyes-García *et al*., 2007).

En el caso de la producción de bebidas fermentadas mexicanas encontramos diversos factores que amenazan la continuidad de estos productos, sin embargo, en el caso particular del colonche encontramos un renovado interés en mantener la producción de este producto. A pesar de que los estados de Zacatecas, San Luis Potosí y Guanajuato actualmente viven un cotidiano ambiente de violencia, falta de seguridad económica, o una fuerte influencia del exterior debido a las altas tasas de migración que ocurren en estas localidades, la producción de colonche se mantiene. En estas localidades ocurre que productores jóvenes mantienen e intentan recuperar esta bebida, que no solo aporta otro producto a la mesa, sino que también es importante en las economías familiares, pues representa un aumento en los ingresos durante la temporada de producción. De igual manera, se fortalece la identidad como comunidad ya que se fomenta su consumo en localidades enteras como es el caso de Laguna de Guadalupe y Mexquitic de Carmona, los cuales se conciben ellos mismos como coloncheros. Asimismo, esta recuperación de la memoria líquida por grupos jóvenes ha generado que las generaciones antiguas que emigraron al extranjero regresen a sus localidades a degustar el colonche e incluso buscar formas para transportarlo a otras regiones. En este sentido, las comunidades a partir de distintos mecanismos son resilientes, a pesar de las distintas presiones, no obstante, esto solo representa un caso puntual y ciertamente muy favorable, pero quedan muchos más productos que deben atenderse.

Lamentablemente, las políticas públicas y las regulaciones gubernamentales también juegan un papel importante en la erosión de los sistemas ecológicos tradicionales. Por ejemplo, se promueve la implementación de sistemas educativos homogeneizadores y generalmente externos, que al paso del tiempo influyen desplazando conocimientos locales (Voeks y Leony, 2004; Cruz García, 2006; Tang y Gavin, 2016; Maffi, 2005; Zent y Maffi, 2009). En este sentido, me refiero a que la implementación del sistema educativo hegemónico reprime y degrada la cultura y la tradición de los grupos indígenas ya que afectan directamente el cambio en las prácticas tradicionales de subsistencia. Promueve la pérdida en las instituciones tradicionales, la pérdida de los derechos tradicionales y al mismo tiempo, la pérdida de los medios de transmisión (Ruddle, 1993; Reyes-García, 2010; Reyes-García *et al*., 2013; Am, 2019).

Respecto a esto último, existe una documentada restricción del uso idiomas locales, lo cual afecta negativamente la transmisión de estos conocimientos subvirtiendo así las libertades nativas de auto asociarse y admitir bienes y tierras en común (Tang y Gavin, 2010, 2016). De hecho, en México, esto es una laguna clave de la reforma, aún vigente, al artículo 27 de la constitución, permitiendo la compra-venta de tierras ejidales, negando así la capacidad de auto asociarse y admitir bienes y tierras en común. En el caso de las bebidas fermentadas tradicionales mexicanas no se tiene un registro directo en donde se pueda atribuir la relación entre la pérdida directa de la producción de estas bebidas y el sistema educativo, no obstante, esto es un aspecto que debe considerarse en futuras investigaciones. Así mismo, si bien la regulación de estos productos permite o garantiza la calidad de estos productos para distintos consumidores, algunas regulaciones de tipo administrativo-económico juegan un papel clave para desincentivar la producción de bebidas como el pulque y el mezcal. Por otro lado, los incentivos como las denominaciones de origen si bien incentivan la producción en ciertas localidades, tienen un efecto negativo en otras que económicamente no cumplen los requisitos, es decir las marginalizan. En la actualidad, los impuestos ejercidos para los productores de mezcal representan un panorama complicado para la amplia diversidad de productores y particularmente para los pequeños productores, que enfrentan una mayor complejidad ejercida por el mercado para que sus productos prevalezcan.

Asimismo, los pueblos o naciones que han sido históricamente colonizados han cambiado los procesos de adquisición, mantenimiento y expansión de las vías de transmisión, debido a la erosión y limitación de estos, lo que ha llevado a la pérdida de los rituales asociados, los privilegios tradicionales y la pérdida de los espacios tradicionales, es decir, los desplazamientos de grupos culturales, las restricciones de los espacios como tierras tradicionales y el acceso a los recursos (Phillips, 1997; Rockman, 2003; Battiste 2008). El ejemplo más característico de esto es la producción del pulque en el país. Esta bebida ha pasado por una dramática reducción en las zonas de producción y particularmente por sanciones establecidas posterior a la colonización española (Escobar, 2021; Aquino *et al.*, 2021; del Carmen Navarrete-Torres y Muñoz-Aparicio, 2021). Esto mismo pudo haber ocurrió con el colonche, particularmente en el estado de San Luis Potosí, en donde la iglesia prohibió la producción y el consumo de estas bebidas y se sustituyó por la producción de vinos de uvas que provenían de Europa (Barbosa, 2004; Sierra Garzón, 2011; Rivas y González, 2017). En la actualidad, el contacto con otros grupos culturales puede influir en los medios de transmisión, por ejemplo, se han registrado las implicaciones que tiene la televisión y otros medios que influyen en los intereses de los jóvenes nativos descubriendo así distintas formas de vida y cultura (Minol, 2000; Tang y Gavin, 2016). No obstante, en el caso del colonche, son algunos grupos de jóvenes quienes están rescatando estas bebidas en la actualidad, principalmente como un motivo de identidad y como un producto que puede apoyar económicamente a su familia. En el caso de las bebidas fermentadas tradicionales ocurre que bebidas como el pulque, el colonche, el tepache el pozol, entre otros, sean motivo de verse como productos de un estatus bajo, e incluso han llegado a ser sustituidos por otras bebidas. Esto puede deberse principalmente a las ampliaciones de los mercados nacionales e internacionales, es decir, el aumentar la disponibilidad de los productos industrializados en las comunidades y se reduce la transmisión de los conocimientos sobre los medios de producción de alimentos en estas pequeñas comunidades (Godoy *et al*., 1998; Reyes-García *et al*., 2007). Del mismo modo, las demandas impulsadas por el mercado pueden generar cambios bruscos hacia bienes externos que son vistos como valiosos en comparación con las especies y los alimentos cosechados tradicionalmente (Soemarwoto, 2007).

A través de la fermentación y el conocimiento ecológico tradicional asociado a este proceso se pueden encontrar estrategias de adaptación para la seguridad alimentaria. En este sentido, realizar acciones locales que promuevan el mantenimiento de la transmisión de los conocimientos ecológicos tradicionales, mantener los ambientes de donde obtienen los recursos deben ser factores clave para garantizar la continuidad de estos productos. Y no deben ser descuidados por ganancias políticas o comerciales, o abandonados ante los complejos panoramas establecidos por la violencia y las presiones económicas del mercado, estos deben atenderse, buscando el bienestar de pueblos y comunidades tanto indígenas como no indígenas. Si bien identificamos la ausencia en la literatura de bebidas fermentadas como la producción del vino mezquite, estas pueden ser retomadas a través de trabajo en campo, observación participativa, entre otras actividades como se ha detectado en otros trabajos (Cano y Suárez, 2020). No obstante, estas deben de ir acompañadas con política pública bioculturalmente pertinente y una mayor atención de la comunidad académica que apoye a las comunidades productoras ya que ellos son los responsables de mantener estos sistemas de conocimiento. Hay que señalar que estos espacios fermentativos promovidos por el ser humano mantienen recursos genéticos útiles para el ser humano, los cuales han sido escasamente estudiados. Además, la interacción de los conocimientos tradicionales y la ciencia pueden proveer importantes respuestas a futuros y complejos escenarios.

El manejo de comunidades de microorganismos, la relevancia de aportar evidencia para una teoría del manejo.

Si bien los estudios del manejo han sido ampliamente dirigidos al estudio de plantas, animales y en menor grado a hongos, el estudio de los microorganismos es mucho menor. No obstante, estudiar las comunidades microbianas en productos fermentados es relevante en términos conceptuales ya que brinda perspectivas para entender las implicaciones de manejo, permite vislumbrar procesos evolutivos, como lo son la domesticación y selección de microorganismos, así como en términos económicos y en cuestiones de las diversas aplicaciones biotecnológicas que derivan del estudio de estos grupos. A través del estudio de bebidas fermentadas y particularmente los resultados obtenidos a partir de la caracterización del colonche se puede plantear que el manejo de microorganismos tiene distintas implicaciones y que corroboran que existen prácticas de manejo que actúan en distintas escalas sobre las comunidades de microorganismos, es decir, tanto en consorcios de microorganismos y a nivel de linajes específicos.

Como se mencionó en la Introducción General de esta tesis, los productores de alimentos y bebidas fermentadas llevan a cabo diferentes prácticas para elaborar los diversos productos fermentados, muchas de estas prácticas permiten tanto controlar el número y los tipos de organismos que están presentes en la fermentación. Estas prácticas son similares a lo que ha sido descritas en comunidades de plantas y animales por ejemplo en el caso de *Anoda cristata* y *Crotalaria pumila*, plantas herbáceas que son favorecidas por las comunidades de variantes reconocidas como “hembras” (Casas *et al.*, 2007). Por ejemplo, en el caso del colonche se observó que a través de la selección de inóculos se controla tanto el número de microorganismos como los tipos de microorganismos. En estas muestras se mantiene un número alto de levaduras de *Saccharomyces* pero no se promueve otro grupo de levaduras, asimismo, se favorece únicamente el desarrollo de bacterias ácido lácticas. De igual manera, se puede observar que la cocción del sustrato contrario a lo esperado promovería una reducción en la riqueza y diversidadde microorganismos, pero debido a que este proceso no involucra una esterilización es probable que solo se promoviera que los azucares estuvieran más disponibles a otros grupos microbianos y por esa razón se observó un mayor número en comparación a las muestras finales del colonche.

Uno de los resultados más importantes es la composición de la comunidad obtenida en las ollas de fermentación donde se realiza la fermentación del colonche, la cual despliega una amplia diversidad tanto de bacterias como de hongos. Particularmente estos resultados son relevantes debido a que permiten visualizar que los productores realizan un cuidado de los microorganismos que están en la olla, a través de su limpieza sin agentes químicos, designándole un espacio particular en la casa para que se mantengan libres del exterior y al final resultan en espacios donde también se almacenan microorganismos que van a continuar en la fermentación del colonche. Esta práctica es similar a lo previamente descrito por Casas y colaboradores (2007) en donde se fomenta el crecimiento y la protección de algunos individuos vegetales y particularmente se protege a las especies de plantas útiles. Lo que puede implicar en algunos casos selección artificial plantas individuales y si esto lo ponemos en una perspectiva de manejo de microorganismos, el manejo de las ollas permiten fomentar el crecimiento y proteger microorganismos *in situ*.

Interacciones microbianas y futuras direcciones para su estudio en bebidas fermentadas tradicionales

Como en cualquier ecosistema natural, los microorganismos en las fermentaciones de alimentos exhiben diversas interacciones ya sean positivas o negativas. De igual manera, estos interactúan con las matrices fermentables y el ambiente en el que se encuentran (Viesser *et al*., 2021; Flachs y Orkin 2021; Johnson *et al*., 2021, Tsitouras *et al.*, 2022).Todas estas interacciones contribuyen a su desarrollo mutuo porque dentro de estos entornos ocurren interacciones de bacterias-bacterias, bacterias-levaduras, levaduras-levaduras e interacciones de hongos filamentosos-levaduras (Liu *et al*. 2017), contribuyendo a la producción de alimentos fermentados seguros y con una amplia diversidad de sabores. Si bien en el presente proyecto no se abordó el estudio de las interacciones de la comunidad de microorganismos en el colonche en un sentido estricto, el diseño experimental elaborado en el tercer capítulo permite entrever que ocurren cambios en la comunidad de microorganismos las cuales permiten hacer ciertas inferencias respecto a sus interacciones. Por ejemplo, se puede observar en el caso de fermentaciones espontáneas, la olla presenta un alto número de microorganismos que pueden llegar a ser patógenos, noobstante, la presencia de un alto número de bacterias ácido-lácticas posiblemente asociadas a los frutosde *O. streptacantha* que predominan en el producto final están relacionadas a promover un ambiente selectivo donde estos patógenos no pueden desarrollarse.

Así mismo, la dominancia de bacterias ácido-lácticas en el inóculo podría inhibir el crecimiento de algunos organismos patógenos que provienen del tratamiento de cocción previo que realizan con los frutos de *O. streptacantha*. Es importante señalar que los estudios de interacciones *in vivo* son relativamente pocos, pero son de amplia importancia ya que permiten ver los recambios de comunidades en tiempo real como ha sido abordado en distintos quesos (Salva *et al*., 2011; Scatassa *et al.*, 2017; Yu *et al.*, 2020; Rolim *et al.*, 2020). Así mismo, una diversa gama de herramientas "ómicas" o reconstrucciones comunitarias *in vitro* permiten revelar los mecanismos moleculares que impulsan la sucesión microbiana e identificar el papel de las interacciones microbianas en los cambios de la composición de la comunidad en el tiempo en productos como las masas madres, quesos e incluso en la fermentación de té (Weckx *et al*., 2019; Zhao *et al*., 2019; Lee *et al.*, 2020; Hu *et al*., 2021). En la actualidad estas herramientas han sido empleadas en diversos productos. Quizá uno de los más estudiados es el queso, ya sea Roquefort o queso azul, en el cual se ha observado los cambios en las comunidades de la corteza, la interacción enzimática entre el hongo *Galactomyces* y cuatro géneros de Proteobacteria, así como con mohos y actinobacterias bajo diferentes condiciones ambientales, tanto como humedad y en secas (Irlinger y Mounier 2009; Wolfe *et al*., 2014). Además, experimentalmente para evaluar la fuerza y la resiliencia de ciertos consorcios microbianos, se realizan reconstrucciones cocultivando bacterias y los hongos más abundantes, es decir, se ponen a prueba la eficacia de los inóculos (Lu *et al.*, 2016; Chai *et al.*, 2020). La identificación de patrones de interacción en las comunidades microbianas proporciona una base para la mejora de los productos, el análisis en profundidad de las interacciones microbianas acelera aún más el desarrollo de tecnologías de fermentación y promueve la transformación inteligente de la fermentación de alimentos y bebidas en general.

Señales de selección artificial, las bebidas fermentadas como espacios para abordar el estudio de domesticación de microorganismos

Los procesos de domesticación son procesos evolutivos que se encuentran íntimamente ligados al aprovechamiento diferencial de la variabilidad morfológica, genética y funcional que existe en las poblaciones de seres vivos (Casas *et al.*, 2007; Zizumbo-Villarreal y Colunga-Gacía Marín, 2010; Mayerr *et al.*, 2015; Pickersgill, 2016 Pérez-Jaramillo *et al*., 2016). Tales procesos están fuertemente relacionados con las culturas las cuales establecen distintos patrones de uso y manejo de los recursos, influenciadas por los distintitos contextos socio ecológicos en los que viven (Clutton-Brock, 1992; Casas *et al*., 2007; Zizumbo-Villarreal y Colunga-Gacía Marín, 2010; Bonavia, 2013; Pickersgill, 2016;Ellen y Fukui, 2021). Si bien durante esta tesis no se llegó a la evaluación de un consorcio de microorganismos o un linaje especifico que pudiera estar bajo selección artificial, la información presentada en el caso particular del colonche permitió incorporar información referente a los procesos de selección de estos consorcios y en últimas consecuencias en linajes específicos. Por ejemplo, la presencia de una dominancia de bacterias ácido-lácticas en los inóculos nos puede dar rastros de selección a nivel de consorcios, mientras que la presencia de solo un género de levaduras como es el caso de *Saccharomyces*, nos permite vislumbrar la selección a nivel linajes. En este sentido, es claro que el manejo de microorganismos ocurre y a pesar de que no opera a escala macroscópica omorfológica como en el caso de poblaciones de animales o plantas, las implicaciones pueden verse también en el cambio de las frecuencias tanto de riqueza, diversidad y dominancia en la comunidad debido al manejo.

Si bien este trabajo no tiene el alcance para dilucidar posibles síndromes de domesticación tanto para consorcios microbianos o linajes específicos, este proyecto permite corroborar que la elaboración de inóculos es un proceso clave en la selección de ciertos consorcios microbianos y un linaje específico como es el caso de *Saccharomyces*. Así mismo, en el caso de fermentaciones espontáneas, ocurre que, debido a las características de la olla y su limpieza, un cierto grupo de microorganismos permanece o son seleccionados al final de la fermentación espontánea del colonche y se mantienen en la olla. Entonces, esto puede verse como una fermentación híbrida ya que, por un lado, es una fermentación que en sentido general es espontánea, pero, por otro lado, los cuidados que tienen los productores con la olla, permite que la olla oriente la inoculación Para redondear esta idea, es que a través de estas prácticas hay indicios de selección de ciertos consorcios y que tiene sus implicaciones para la elaboración del colonche. Esto ocurre en las actuales búsquedas de consorcios microbianos para desarrollar mejores productos a una mayor velocidad en productos a escala industrial (Buckenhüskes, 1993; Sunesen y Stahnke, 2003; Johansen, 2018; Guerrini *et al*., 2021). Quizá futuros estudios pueden abordar la robustez de estos consorcios para probar la importancia de esta selección guiada por el conocimiento tradicional y corroborar que este proceso de seleccionar inóculos es una vía que promuevela domesticación a nivel comunidad.

Particularmente en el caso del colonche elaborado con el uso de inóculos, los productores denominan a esta matriz microbiana como xinaiste o cinaiste. Estos son conocidos como las madres para la fermentación de sus colonches y si bien no hay un conocimiento directo de que microorganismos están presentes, es decir no asignan nombres comunes como ocurre con plantas o animales, los productores asumen que hay “algo” que fermenta o hierve al producto. Si bien, no ocurre esta designación de nombres comunes, pero quizá el designar a estos inóculos con un nombre en particular puede ser considerado como un caso similar en donde la selección opera a nivel de comunidad. De igual manera, estos productores saben que mantener estos productos en el refrigerador va a permitir que el próximo año la fermentación se realice de manera más rápida debido a que se queda la esencia de la fermentación en estos inóculos.

En el caso de la selección de linajes específicos, la levadura *Saccharomyces cerevisiae* es sin duda la especie más estudiada en productos fermentados, con una importancia económica e histórica para el ser humano y a la cual se han identificado señales de domesticación (Gallone *et al*., 2018; Preiss *et al.,* 2018; Lahue *et al.,* 2020; Pontes *et al*., 2020; Bigey *et al*., 2021; Han *et al*., 2021). Actualmente la propuesta de domesticación en esta especie plantea que las especies de *S. cerevisiae* asociadas a producciones industriales y bajo esquemas de fermentaciones como es el caso de las mono cepas en la industria cervecera presentan señales de domesticación asociadas a una selección de atributos específicos para producir una cerveza específica (Gallone *et al*., 2018; Preiss *et al*., 2018; Han *et al*., 2021). Los cambios que se han descrito, son cambios asociados en rutas metabólicas, una mayor especificidad a fuentes de carbono, una mayor presencia de pseudogenes, la ausencia de genes asociados a patogenicidad y una marcada falta de capacidad reproductiva vía sexual (Steensels *et al*., 2019; Gallone *et al*., 2019; Han *et al*., 2021; Bigey *et al*., 2021; Bai *et al*., 2022) Estos cambios en el genotipo y fenotipo se atribuyen a una selección relajada atribuida a un ambiente homogéneo favorecido por el ser humano, un ambiente que generalmente está libre de competencia (Peter *et al*., 2018; Steensels *et al.*, 2019, 2021; Gallone *et al*., 2019; Lahue *et al*., 2020; Fatma et al., 2020). En un estado incipiente de domesticación se encuentran las cepas de *S. cerevisiae* provenientes de fermentaciones por inóculos en las cuales hay una mayor homogeneidad en el ambiente, y la interacción entre otros microorganismos ocurre, a diferencia de las fermentaciones industriales, estas cepas ya presentan cambios en rutas metabólicas, no obstante, aún muestran capacidad de reproducción sexual y no solo por gemación (Steensels y Verstrepen, 2014). Estas cepas han sido caracterizadas en bebidas como el sake, vinos y cervezas más tradicionales. Finalmente, en este último gradiente de domesticación se encuentran las cepas relacionadas a fermentaciones espontáneas o silvestres (Gibbons y Rinker, 2015, Gallone *et al*., 2016). Aquí aún existe la presencia de producción de sabores desagradables, pero una mayor supervivencia en la naturaleza y reproducción sexual.

Si bien el alcance del presente proyecto no permitió evaluar señales en el fenotipo o genotipo de domesticación en las especies de *S. cerevisiae* en las fermentaciones tanto espontáneas como de inóculos del colonche, futuros proyectos pueden abordar el estudio de estas cepas. Al existir una amplia diversidad de bebidas fermentadas y sustratos con las que se elaboran estas bebidas, es posible que explorar con cepas de *S. cerevisiae* asociados a sustratos provenientes de fermentaciones de agaves, maíz o cactáceas, así como, de distintas prácticas de manejo permita fortalecer la evidencia del conocimiento tradicional, la importancia del manejo en la comunidad de microorganismos y dilucidar los procesos que llevan a la domesticación de este pequeña pero tan importante especie. Igualmente, caracterizar genotípica y el fenotípicamente de estas levaduras puede brindarnos información respecto a la especificidad de fuentes de carbono de estas y quizás, así como mejorar los procesos de producción de las bebidas en las que son empleados. investigaciones abrirían paso a que estos microorganismos involucrados en fermentaciones tradicionales sean considerados en la política pública donde se promueva su resguardo y que se realicen acciones de prevención ante la biopiratería.

Perspectivas para generar políticas públicas para la conservación y la promoción de fermentos y la conservación de microorganismos

Uno de los temas que no debería pasar por alto en la actualidad en relación con el manejo de los recursos biológicos es la protección de los recursos y conocimientos tradicionales de los pueblos indígenas. Actualmente existen marcos legales que no brindan una protección adecuada, ni garantizan la apropiación de terceros a través de sistemas de propiedad intelectual (Ho, 2005; Nordin *et al.*, 2012). Si bien el Convenio sobre la Diversidad Biológica introdujo la obligación de solicitar el uso consentido previo para el uso de cualquier conocimiento tradicional y garantizar distribución de beneficios, el sistema de propiedad intelectual existente no tiene el requisito de distribución de beneficios, tampoco fue diseñado para la protección de los conocimientos tradicionales en su forma original (es decir, en su existencia oral y sin documentación) (Chiarolla, 2009, Kim, 2010). Tales características hacen que el conocimiento tradicional sea inaccesible para la inspección por parte de los oficiales de patentes y por lo tanto dejan un camino corto y sencillo a la biopiratería, que aprovechan estas lagunas legislativas y les son concedidas patentes sobre innovaciones que se basaban en conocimiento previo generado por otros grupos humanos (Murphy, 2001; Pila, 2003).

Existen millones de variedades de plantas, animales y microorganismos en el mundo hoy en día (Jackson *et al.*, 1992; Caliskan 2012; Thomas, 2013; Satyanarayana *et al*., 2013; Stoy *et al*., 2015). Ni siquiera sabemos el número de especies que viven en este planeta e incluso nuevas especies son descubiertas año con año (Corlett, 2016; Thomas, 2013; Crist, 2019; Nic Lughadha *et al.*, 2020). No obstante, al registrar el conocimiento tradicional, legalmente, se convierte en conocimiento de dominio público. Según la ley de patentes, esto significa que se considera como una técnica previamente utilizada y, por lo tanto, no es patentable (Udgaonkar, 2002). Dicho registro escrito, en un formato de fácil acceso para las oficinas de patentes de todo el mundo, proporcionaría a todas esas oficinas un registro del estado de la técnica ya sea algo previamente implementado en cualquier región del mundo (Kim, 2021). Los encargados de dictaminar las patentes a través de las bases de datos pueden examinar si en efecto es un producto nuevo o la mera copia de conocimiento tradicional.

En el caso de la elaboración de productos fermentados o de microorganismos, las lagunas son enormes, pocos estudios han dado importancia al registro de los procesos de producción, así como los microorganismos involucrados (ten Have, 2021; Mukku *et al*., 2021). Por esta razón, la presente tesis se dirigió a documentar estos productos y buscar que sean respetados como parte de conocimientos tradicionales, ya que no solo representan posibles beneficios para la industria, sino que para toda la humanidad. Estos conocimientos son básicos para el desarrollo de una amplia gama de productos, estos son conocimientos valiosos y no deben ser tomados a la ligera. Por esta razón, la buscamos evidencia de los procesos de fermentación, la selección de los sustratos involucra saberes y conocimientos del ambiente en donde se reproducen estos productos y con menor frecuencia considerados, también en los microorganismos involucrados. Las políticas públicas hacia la producción de alimentos y materias primas deben basarse en el conocimiento y aprovechamiento de la biodiversidad, su protección y el reconocimiento de los derechos de propiedad intelectual y territorial de las culturas que por miles de años los han desarrollado (Casas y Vallejo, 2017)

Particularmente en México es prioritario revisar a fondo las políticas de conservación de la biodiversidad. Decretar áreas naturales protegidas no es suficiente para garantizar su conservación, es imperante hacer una revisión detallada de los criterios para proteger *in situ* las especies en general y aquellos que representan recursos genéticos de alta prioridad nacional, entre los cuales se encuentran los microorganismos, plantas y grupos culturales abordados en esta tesis. Los principales reservorios de diversidad genética de estos se encuentran en las localidades productoras, las cuales han sido marginalmente consideradas para las políticas de conservación y esta tesis es un intento para identificarlos y protegerlos. Asimismo, el inventario de tecnologías para el manejo de los recursos bióticos debe acompañarse con un esfuerzo nacional por documentar, sistematizar, especializar y utilizar en la planeación, los sistemas de producción de alimentos fermentados desarrollados por las culturas nacionales por miles de años. Esta estrategia no solamente es una deuda con los pueblos de México, sino también la base para una reconstrucción tecnológica que ha demostrado mayor eficacia que las tecnologías modernas en conciliar la producción con la conservación de agrobiodiversidad (Casas y Parra, 2016; Casas *et al*., 2016, 2017; Casas y Vallejo, 2017).

Conclusiones

Las bebidas fermentadas tradicionales de México son reservorios de una amplia diversidad biocultural, estas mantienen y fomentan altos niveles de riqueza y diversidad de especies vegetales que van desde plantas domesticadas a plantas silvestres. Además, son productos íntimamente relacionados con diversos grupos culturales, ya que son ellos quienes mantienen y promueven estas bebidas, las adaptan a nuevas tecnologías, incorporan diversas materias primas, se les da un sentido de patrimonio alimentario e identidad social. Así mismo, es en estas comunidades donde se expresan los conocimientos milenarios resultado de la estrecha relación del ser humano y su ambiente lo cual se expresa en los diversos recursos vegetales empleados para elaborar y modificar estos microespacios. También, con una menor visibilidad, estos espacios albergan una amplia diversidad de microorganismos de los cuales al igual que las comunidades vegetales los seres humanos consciente o inconscientemente realizandiversas prácticas de manejo para elaborar productos únicos en distintas localidades del país. Asimismo, la diversidad de alimentos fermentados, varían según el área geográfica y la preferencia cultural, se producen en un gran número de estados del territorio nacional y las características individuales y peculiares que distinguen y tipifican cada producto están determinadas por la expresión de la amplia biodiversidad de los microorganismos fermentadores y actualmente este estudio aporta información base para describir la esencia del colonche.

Un aspecto común entre las bebidas fermentadas tradicionales y que particularmente se identificó en el colonche es la presión socio-cultural a la que están sometidos. Diversos factores ponen en riesgo la continuidad de la producción de estos productos, la falta de transmisión de este conocimiento, la restricción a los recursos para elaborarlos, la presión del mercado ante la entrada de productos sustitutos como otras bebidas fermentadas o los refrescos son los factores generales que afectan la pérdida de bebidas fermentadas tradicionales y que fue visible en el caso del colonche. De igual manera, diversos factores de presión condicionan la elaboración de estos productos en cada localidad productora. Sin embargo, un sentido de apropiación a las bebidas fermentadas tradicionales locales ha permitido mantener un nuevo interés en la producción de estas y es que en estas comunidades se ejerce una constante lucha para mantener estos espacios libres del desarrollo intensivo y se mantienen al día con su integridad cultural y ecológica.

La presente investigación mostró que colonche es un término genérico que comprende a un grupo diverso de bebidas fermentadas, con variaciones locales y regionales. Esta diversidad nosolamente se relaciona con las diferentes especies de cactáceas cuyos frutos se involucran. También contribuyen los contextos culturales de su preparación y los ambientes en los que conviven humanos, cactáceas y microorganismos involucrados. Las diferentes técnicas de manejo son expresiones de siglos de historia, de cambios culturales y tecnológicos y muestran que influyen en cómo son los consorcios de microorganismos que intervienen en la fermentación. Los contextos sociales y ecológicos, culturales y biológicos se encuentran entrelazados lo mismo a escala de los paisajes forestales y agrícolas que en los asentamientos humanos que ocupan los pobladores, así como en los micro-paisajes que se construyen en cada técnica de preparación. Una bebida es la síntesis de biología, cultura y procesos multiescalares. En este sentido, realizar medidas como la proposición de zonas con denominación de origen como ocurre en el caso del mezcal restringe a todos las expresiones locales y regionales que pueden experimentarse para la producción de los colonches. Así mismo, deben de ser cautelosas las propuestas de la elaboración de patentes, tanto del producto como de los microorganismos asociados a su fermentación.

La caracterización de las comunidades microbianas relacionadas con la producción de distintos colonches elaborados a partir de frutos de *O. streptacantha* bajo los tratamientos de fermentaciones espontáneas e inoculadas permiten confirmar que las prácticas de fermentación muestran cambios en la riqueza de especies, la diversidad y la estructura de la comunidad bajo estos tratamientos. A pesar de que las diferencias son ligeramente significativas para las comunidades bacterianas y fúngicas en los productos finales los colonches producidos no presentan posibles organismos patógenos y esto puede deberse al amplio número de bacterias ácido-lácticas y la dominancia de levaduras del género *Saccharomyces*. De igual manera, el estudio de los inóculos con los que realizan la fermentación del colonche permite confirmar que existe una selección continua sobre las comunidades microbianas y que se reduce la comunidad microbiana donde se seleccionan mayoritariamente bacterias ácido-lácticas y *Saccharomyces* para futuras fermentaciones. Finalmente, brinda una perspectiva distinta a las fermentaciones espontáneas, debido a que el estudio de los contenedores donde se realiza son reservorios de microorganismos para las futuras fermentaciones y las prácticas del cuidado de las ollas por parte de los productores garantiza su continuidad. En general, este estudio brinda información sobre el conocimiento y el manejo tradicional sobre comunidades de microrganismos para elaborar bebidas fermentadas y por lo tanto, a importancia de mantener estos productos, las prácticas y la diversidad asociada durante los procesos de producción de estos elementos dentro de la gastronomía mexicana.

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