UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

DOCTORADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE ECOLOGÍA

ECOLOGÍA

EFECTO DE LAS INTERACCIONES ECOLÓGICAS DE ALTO ORDEN EN LA ESTRUCTURA Y FUNCIONAMIENTO DE LA RED DE UN CAFETAL

TESIS
QUE PARA OBTENER EL GRADO DE DOCTORA EN CIENCIAS

PRESENTA:
CECILIA GONZÁLEZ GONZÁLEZ

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Ciudad Universitaria, Cd. Mx., marzo 2024

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COORDINACIÓN GENERAL DE ESTUDIOS DE POSGRADO
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M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Por medio de la presente me permito informar a usted que el Comité Académico del Posgrado en Ciencias Biológicas, en su sesión celebrada el **19 de junio del 2023** aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la estudiante **GONZÁLEZ GONZÁLEZ CECILIA** con número de cuenta **308756676,** con la tesis titulada**: "EFECTO DE LAS INTERACCIONES ECOLÓGICAS DE ALTO ORDEN EN LA ESTRUCTURA Y FUNCIONAMIENTO DE LA RED DE UN CAFETAL",** bajo la dirección de la **DRA. MARIANA BENÍTEZ KEINRAD**, Tutora Principal, quedando integrado de la siguiente manera**:**

Presidente:	DRA. KARINA BOEGE PARÉ
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Secretario:	DR. DENIS PIERRE BOYER

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

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 04 de marzo de 2024

COORDINADOR DEL PROGRAMA

DR. ARTURO CARLOS II BECERRA BRACHO

c. c. p. Expediente del alumno

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Al Posgrado de Ciencias Biológicas de la Universidad Nacional Autónoma de México.

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Para Yolanda

ÍNDICE

RESUMEN

Uno de los campos de investigación más activos en la Ecología es aquél que busca entender los mecanismos que generan y sostienen la alta biodiversidad que observamos en muchos de los ecosistemas del mundo. Las interacciones que sostienen entre sí los organismos vivos son la espina dorsal de dichos sistemas y, como tal, han estado en el foco de estas investigaciones. A través de las décadas, hemos aprendido mucho sobre la forma en que se estructuran las comunidades y cómo distintos tipos de interacción, como la competencia, la depredación y el mutualismo, afectan su funcionamiento. En los últimos años se ha estudiado crecientemente una forma más en que los organismos se relacionan entre sí, a través de las llamadas interacciones de alto orden (HOI por sus siglas en inglés). Este tipo de interacciones ocurren cuando una especie modifica la interacción entre otras dos o más especies, sin la necesidad de afectar en primer lugar la densidad de ninguna de ellas. Por su ubicuidad en la naturaleza y por la gran cantidad de efectos que éstas desencadenan, se ha propuesto que las HOI pudieran ser uno de los mecanismos importantes para moldear y sostener la biodiversidad en las comunidades biológicas. En esta tesis, nos propusimos poner a prueba esta idea mediante la investigación del efecto de las HOI en el funcionamiento de un sistema cafetalero descrito empíricamente y representado como una red ecológica. En primer lugar, realizamos una revisión bibliográfica sobre lo que se sabe del impacto de las interacciones ecológicas de distintos tipos sobre el funcionamiento de las comunidades, con un énfasis en los estudios de redes ecológicas. Con ella aprendimos que existe una enorme diversidad de resultados, en muchos casos contradictorios, sobre la relación entre la estructura de las comunidades y su funcionamiento. Dicha contradicción parece en parte provenir de la gran variedad de metodologías de investigación y de las limitaciones que cada una conlleva. Aprendimos también que existen metodologías novedosas que pretenden integrar de mejor manera diferentes tipos de interacción, así como una mayor cantidad de otros factores y que ofrecen una vía para tratar de dar sentido a las observaciones previas; entre estas metodologías, aquellas capaces de incorporar las interacciones de alto orden resultan prometedoras. Después definimos nuestra propia red ecológica a través de la revisión e integración de numerosos estudios sobre las interacciones que se conocen en un cafetal determinado de la zona del Soconusco, Chiapas. Esto nos dio como resultado una red con 22 nodos. A partir de lo que aprendimos con la revisión, decidimos estudiar esta red desde metodologías complementarias. Primero hicimos un análisis de la robustez de la estructura de la red ante distintos escenarios de pérdida de nodos y encontramos que cuando se agregan las interacciones de alto orden, la red es más robusta que cuando se trabaja con la red que únicamente incluye interacciones de primer orden. Cabe señalar que para realizar este análisis fue necesario proponer un método para incorporar las HOI en la estructura clásica de las redes matemáticas, así como modificar un índice de robustez conocido para poder incluirlas. Después, agregamos a la red una dimensión dinámica mediante la modelación de sus densidades poblacionales con una ecuación de tipo consumidor-recurso extendida para

incorporar HOI. En diálogo con el experimento puramente estructural, investigamos la supervivencia de la comunidad y la abundancia de sus componentes ante la pérdida de nodos. Además, por un lado realizamos el experimento de remover interacciones de primer orden, es decir, interacciones directas (depredación, competencia, mutualismo, parasitoidismo, etc.), y por otro lado removimos interacciones de alto orden. En contraste con los resultados de robustez estructural, con la modelación dinámica no se detectó un efecto significativo de la presencia o ausencia de HOI sobre la supervivencia de la comunidad, ni sobre las abundancias de determinadas especies. Además, el experimento de remoción de interacciones arrojó que eliminar interacciones de primer orden tiene un efecto negativo sobre la supervivencia de las especies, mientras que eliminar las interacciones de alto orden tiene un efecto positivo. En conclusión, si bien esta tesis no nos permite dar una respuesta concluyente sobre la relevancia de las HOI para el funcionamiento de la red del cafetal estudiado, sí nos permitió avanzar propuestas metodológicas para incorporar las HOI en los estudios de redes tanto estructurales como dinámicos y matizar el papel que se le ha atribuido a las HOI para mantener la diversidad de las comunidades. También, nuestros resultados evidencian con un mismo sistema de estudio la necesidad de abordar nuestras preguntas desde metodologías que se complementen entre sí y de tomar con precaución lo que pueden ser conclusiones prematuras sobre el papel de las HOI en el funcionamiento de las comunidades.

ABSTRACT

One of the most active fields of research in Ecology has been that which seeks to understand the mechanisms that shape and sustain the high biodiversity that we find in many of the world's ecosystems. The interactions that organisms have with each other are the spinal cord of these systems, and as such, they have been at the center of these investigations. Through the decades, we have learned much about the way in which communities are structured and how different kinds of interactions, such as competence, predation and mutualism, shape their dynamics or their functions. Recently, a new way in which organisms relate to each other through the so-called high order interactions (HOIs) has been increasingly studied. These interactions are those in which one species modifies *the interaction* among two or more other species, without the need to modify their densities in the first place. Because of their ubiquity in nature and the large amount of effects that they unchain, it has been proposed that HOIs may be one of the most important mechanisms that shape and sustain biodiversity in ecological communities. In this thesis, we set ourselves to test this idea through the study of the effect of HOIs in the functioning of an empirically-known coffee agroecosystem, represented as a network. First, we reviewed information on what is known about the effects of different kinds of ecological interactions on ecological communities, with an emphasis on network studies. With this we learned that there is a huge amount of studies with different findings, in many cases contradictory, on the relationship between the structure and function of communities. These contradictions appear to be at least partly due to the variety of methodologies employed and the limitations that each conveys. We also learned that there are novel methods that try to integrate different kinds of interactions and a larger number of other factors, thus offering a way to make sense of previous findings; among these, those which allow for the inclusion of HOIs are promising. Afterwards, we defined our own ecological network through the revision and integration of numerous studies that uncover the interactions in a specific coffee system in the area of the Soconusco, Chiapas. This resulted in a network with 22 nodes. Accordingly to what we learned with our review, we decided to study the network through complementary methodologies. First we analyzed the robustness of the web's structure in the face of different node-removal scenarios and we found that when HOI are considered, the web is more robust than when only first order interactions are included. In order to perform this analysis we had to propose a method to include HOIs in the classic structure of mathematical networks, and to modify a known robustness index. Afterwards, we incorporated a dynamical dimension to our web through the modeling of its population densities with a consumer-resource equation extended to include HOIs. In a dialogue with the purely structural experiment, we studied the community's survival and the abundance of its components in the face of node removal. In addition, we performed the experiment of removing first order interactions on the one hand, and high order interactions

on the other. In contrast with the structural robustness results, dynamical modeling did not show a significant effect of the presence or absence of HOIs on the community's survival or on the abundance of its species. Additionally, the interaction-removal experiment showed that removing first order interactions has a negative effect on the community's survival while removing HOIs has a positive effect. In conclusion, while this thesis does not allow us to give a conclusive answer to the relevance of HOIs in the functioning of the studied coffee agorecosystem's network, it did allow us to develop some methodological proposals for the inclusion of HOIs in the network studied, both from a structural and from a dynamics perspective, as well as to gain a more nuanced understanding of the role or HOIs in ecosystems. In addition, our results highlight how even when dealing with a single study system, it is necessary to address our questions with methodologies that complement each other.

INTRODUCCIÓN

a. La coexistencia y las interacciones de alto orden

A raíz de la inmensa diversidad de seres vivos que observamos en algunos ecosistemas surge una de las preguntas más relevantes en biología: ¿qué mecanismos permiten la coexistencia de tantos seres vivos en un ambiente compartido? Durante los años cincuenta el entendimiento general en ecología fue que la alta diversidad de organismos era una característica estabilizadora en sí misma, pues la idea era que unas especies controlaban a otras a través de los efectos negativos que ejercían sobre ellas, como en el caso de la competencia y la depredación (Odum 1953; MacArthur 1955; Elton 2020). Esta noción permaneció prácticamente sin cuestionamiento hasta los cincuenta, cuando Robert May (1972; 1973) publicó su hoy clásico trabajo en el cual encontró una relación negativa entre la diversidad de especies y la estabilidad lineal de los sistemas que modeló. La aparente contradicción de este resultado con la observación empírica de sistemas altamente biodiversos desató una enorme cantidad de nuevos estudios que desde entonces han enriquecido nuestro conocimiento sobre la forma en que se ensamblan las comunidades y los mecanismos que permiten la coexistencia de innumerables especies . Siguiendo la iniciativa de May, gran parte de estos estudios adoptaron el uso de las redes y los formalismos matemáticos para representar sistemas ecológicos y analizarlos (Landi *et al.* 2018). En primer lugar, se buscó subsanar las principales simplificaciones y supuestos que el trabajo de May tenía. Así pues, se optó por investigar redes no aleatorias (aunque los estudios con redes aleatorias también continuaron y han brindado importantes conocimientos (Allesina y Tang 2015)). Esto se ha hecho de dos maneras: por un lado, mediante el uso de redes cuya estructura es obtenida mediante observaciones empíricas, y por otro, mediante el uso de modelos que generan redes hipotéticas pero con estructuras similares a las de las redes empíricas. Por ejemplo, el modelo de cascada (Cohen *et al.* 1990) o el modelo de nicho (Williams y Martínez 2000) asignan interacciones entre especies a partir de una serie de reglas matemáticas. En el caso del modelo de cascada, se introducen niveles tróficos jerárquicos de modo que con una probabilidad dada, las especies depredan a aquellas en los niveles inferiores. En el modelo de nicho, las especies se asignan al azar a lo largo de un intervalo y depredan a aquellas asignadas a valores inferiores del mismo intervalo, dentro de una distancia determinada. A raíz de estos trabajos, se ha propuesto una gran cantidad de atributos que son parcialmente responsables de permitir la coexistencia de especies en sistemas ecológicos altamente diversos, los cuales revisamos en el Capítulo I.

Así pues, hoy en día contamos con una gran cantidad de estudios que buscan explicar la existencia de sistemas ecológicos con una gran cantidad de especies. Sin embargo, a pesar de los esfuerzos por sistematizar este conocimiento, la labor ha resultado ser complicada, pues se ha encontrado una multiplicidad de resultados que en algunos casos se contradicen. Por un lado, esto se debe a la complejidad intrínseca de los sistemas vivos, es decir, a los muchos factores que interactúan para dar lugar a los sistemas ecológicos y que frecuentemente resultan en una mayor cantidad de excepciones que de generalidades. Por otro lado, esta falta de consenso también se debe a la enorme variedad de definiciones y metodologías que se han implementado para investigar estas cuestiones y a las limitaciones que cada una conlleva.

En primer lugar, muchos de los estudios que se abocaron a las comunidades altamente diversas lo hicieron mediante el uso de redes ecológicas definidas por especies o grupos de especies que se conectan entre sí mediante un tipo de interacción ecológica, generalmente depredación, competencia o mutualismo. Esto representa una limitante importante debido a que en los ecosistemas reales las especies mantienen todo tipo de interacciones entre sí, por lo que definir las redes a partir de un solo tipo de interacción puede resultar en estructuras poco fieles a la realidad. Otra limitante ha sido la falta de una dimensión de espacio o de tiempo en estos estudios. Como sabemos, las comunidades biológicas cambian a través del tiempo, e incluso en un mismo año. Por ejemplo, es posible que las especies que en temporada seca compiten entre sí, en temporada de lluvias ya no lo hagan. Para capturar cambios de este tipo es necesario incorporar cambios temporales en la estructura de las redes. Del mismo modo, las especies se mueven a través del espacio y esto impacta directamente las interacciones que sostienen en determinados momentos, por lo que incorporar la dimensión espacial puede ser muy importante para la representación de estos sistemas. Por todo esto, desde hace ya algunos años algunos científicos han hecho un esfuerzo por construir redes más integrales, incorporando varios tipos de interacciones ecológicas a la vez (generalmente depredación, mutualismo y competencia), espacio, tiempo u otros factores que originalmente se dejaban de lado. En el Capítulo I ahondaremos en estas innovaciones en los estudios de redes y en lo que nos han ayudado a entender sobre la estructura y el funcionamiento de las comunidades bióticas.

Así pues, a través de los años y haciendo uso de distintas metodologías complementarias, tanto teóricas como prácticas, se han identificado algunos mecanismos y atributos que pueden ser parcialmente responsables de permitir la coexistencia de especies en sistemas altamente diversos. Uno de ellos son las llamadas **interacciones de alto orden (HOI)**, que ocurren cuando una especie modifica la interacción entre otras dos especies, sin necesidad de alterar sus densidades poblacionales (Wootton 1993). Así, las interacciones directas entre dos especies (depredación, competencia, mutualismo, comensalismo, amensalismo) pueden ser llamadas de primer orden, mientras que una modificación a cualquiera de éstas por parte de otra especie se entendería como una interacción de segundo orden. Si la interacción de segundo orden es modificada a su vez por otra especie, hablaríamos de una interacción de tercer orden, y así sucesivamente. Este tipo de interacciones son muy comunes en la naturaleza, y sin embargo han recibido mucho menos atención que las interacciones clásicas (que ahora llamaremos de primer orden) donde dos especies interactúan entre sí modificando sus densidades poblacionales, como en el caso de las relaciones de consumo. Por ejemplo, en la llamada ecología del miedo (Laundré *et al.* 2020) se estudian interacciones de alto orden que se dan cuando un depredador se mueve hacia una nueva área, haciendo con su presencia que las presas potenciales abandonen el sitio, deteniendo su forrajeo y llevándolo a otra zona. En este caso, el depredador, sin necesariamente consumir a sus presas, libera a la vegetación de la zona de la herbivoría a la que estaba sometida, llegando a provocar profundos cambios en el paisaje. En los últimos años, una serie de trabajos pioneros han apuntado a que podría haber una relación positiva entre la existencia de interacciones de alto orden y la capacidad de los sistemas ecológicos de sostener un gran número de especies. Dichos trabajos estuvieron primero basados en sistemas de redes aleatorios, los cuales dialogaron con el estudio ya mencionado de Robert May. Desde entonces, la complejización en el tema ha llevado a la modelación de algunos sistemas empíricos, en su mayoría acuáticos, y unos cuantos sistemas terrestres. Estos estudios parecen confirmar el papel positivo de las HOI para la coexistencia de especies, sin embargo, continúan siendo pocas las investigaciones que han abordado esta cuestión y hace falta complementarlas con más sistemas y más metodologías de análisis (Bairey *et al.* 2016; Kefi *et al.* 2016). Si incluir distintos tipos de interacción de primer orden ha probado ser esencial para entender mejor la dinámica y el funcionamiento de las comunidades, es probable que incorporar también las interacciones de alto orden sea igualmente revelador. En particular, consideramos necesario analizar el papel de las interacciones de alto orden conocidas en más sistemas reales y desde diferentes enfoques metodológicos, con diferentes supuestos y limitaciones, para confirmar la naturaleza de sus efectos sobre el funcionamiento de las comunidades.

b. El sistema de estudio

Los cafetales diversificados son un tipo de sistema agroforestal. Como tales, son formas de uso de suelo que se caracterizan por preservar selectivamente componentes silvestres, generalmente leñosos y perennes, en combinación con el manejo de elementos agrícolas anuales o perennes con niveles avanzados de domesticación. En algunas ocasiones estos sistemas también incluyen el manejo de animales silvestres o con algún nivel de domesticación. El manejo de estos sistemas busca aprovechar y maximizar las interacciones ecológicas entre los elementos forestales y agrícolas del sistema para fines particulares que dependen del contexto ecológico, cultural y económico en el que se encuentran (Moreno-Calles et al. 2013). Para cumplir este objetivo, el manejo depende del conocimiento profundo de los elementos que componen al sistema, los mecanismos mediante los que interactúan, y los fenómenos que de éstos emergen. Este conocimiento es construido contínuamente por los grupos sociales que históricamente han manejado estos sistemas.

Así mismo, desde la ciencia de la ecología, el estudio de las interacciones ecológicas puede aportar una perspectiva complementaria para entender mejor estos sistemas. En este contexto, desde hace alrededor de dos décadas, un grupo de investigación ha seguido de cerca las interacciones ecológicas que se dan en un cafetal altamente diverso de la zona del Soconusco, Chiapas, México. Como resultado, hoy en día se tienen sistematizadas muchas de las especies que conforman este agroecosistema, así como las interacciones que mantienen entre sí. Más aún, existe evidencia de que en este sistema, las interacciones de distintos tipos (depredación, competencia, mutualismo, etc.) y de distintos órdenes (primero, segundo y tercero) juegan un papel determinante en la dinámica del sistema, y en particular, en la regulación autónoma de sus principales plagas potenciales (Vandermeer & Perfecto 2006; Perfecto & Vandermeer 2015). Por lo tanto, éste es un sistema de estudio ideal para poner a prueba aquello de lo que venimos hablando, es decir, para estudiar el efecto de las interacciones de alto orden en el funcionamiento de este agroecosistema. Entender estas interacciones podría guiar el manejo de los cafetales para fomentar aquellos procesos deseables en términos productivos y ecológicos. Sin embargo, antes de entrar en más detalles, conviene hablar un poco más sobre este sistema de estudio.

Debido a los requerimientos ambientales de la planta del café, los cafetales en México se encuentran distribuidos en la intersección entre las regiones neártica y neotropical, una zona biogeográfica bien conocida por ser de las más biodiversas en el mundo. En México, la mayor parte de la producción cafetalera se concentra en las Sierras de Chiapas y Veracruz. Esta ubicación implica que dichos agroecosistemas tienen un alto potencial para impactar a la biodiversidad del país, sea positiva o negativamente. Según un estudio de CONABIO donde se señalan 155 regiones cruciales para la conservación biológica, casi el 10% se sobreponen o están muy cerca de las zonas cafetaleras del país (Moguel y Toledo 1999). Además de la relevancia en términos ecológicos que ésto conlleva, los cafetales tienen también enormes implicaciones sociales y económicas. México es el onceavo país productor más importante de café a nivel global. Como tal, cerca de 560,000 productores dependen directamente de su producción, y si tomamos en cuenta a las familias de los productores y a las personas involucradas en la transformación y comercialización del grano, el número de personas cuya economía depende del café asciende a más de 3 millones. De los productores de café, cerca del 85% son minifundistas pertenecientes a algún pueblo originario (ENA 2017; SAGARPA 2017). Esto genera una alta heterogeneidad espacial que es común en los paisajes donde se practica agricultura campesina, donde las personas trabajan terrenos generalmente menores a 5 ha y lo hacen con una gran variedad de manejos que satisfacen diferentes necesidades económicas y culturales. Este tipo de paisajes comparten entonces características físicas y sociales que los vuelven de altísima importancia para la conservación tanto de la biodiversidad como de la diversidad cultural (Apéndices III, IV, VI). En particular, los cafetales suelen formar parte de mosaicos o matrices heterogéneas de las cuales depende en buena medida que las especies silvestres puedan establecerse temporal o permanentemente y migrar entre parches de vegetación remanente, constituyendo agroecosistemas cuyo manejo resulta determinante para el mantenimiento de la biodiversidad en la escala regional (Apéndices III, V, VI).

En Chiapas, que es el principal estado productor de café en México con más del 40% del volumen anual, este tipo de producción campesina coexiste con otro sistema de producción contrastante: por un lado, podemos encontrar producción de café en fincas de una enorme extensión que emplean mano de obra en un esquema que asemeja al de los antiguos latifundios, y que generan grandes extensiones de tierra con un solo tipo de manejo agrícola, sea orgánico o altamente industrializado. Por otro lado, en el estado están registradas al menos 120 cooperativas indígenas de producción y exportación de café que se agrupan bajo los esquemas de comercio justo, comercio solidario, producción orgánica y autogestión y que además de buscar condiciones más justas para los productores y sus familias, generan paisajes altamente heterogéneos donde las dinámicas ecológicas pueden ser muy diferentes (ENA 2017; SAGARPA 2017). Por estas razones, entender mejor el funcionamiento de estos agroecosistemas, bajo distintos tipos de manejo y esquemas de organización social, es necesario para llevar a cabo acciones que promuevan el bienestar social y ecológico de la región. De igual manera, es crucial entender mejor la respuesta del agroecosistema a posibles cambios en el manejo o a diferentes perturbaciones, tales como la remoción de ciertos elementos y sus interacciones.

En términos de biodiversidad, el café ha sido históricamente cultivado bajo la sombra de un conjunto diverso de árboles propios de las selvas tropicales de nuestro país. Estas plantaciones tienen una alta biodiversidad intencionalmente mantenida por los agricultores, que incluye árboles nativos y a veces también frutales introducidos. Además de esta diversidad planeada, los cafetales contienen una enorme biodiversidad asociada, es decir, especies silvestres que los agricultores no cultivan de manera intencional pero que son capaces de establecerse temporal o permanentemente en estos agroecosistemas. Desde 1990, decenas de artículos han presentado información sobre la alta diversidad presente en los cafetales diversificados (Manson et al. 2008; Arias et al. 2012). Por ejemplo, en un estudio sobre insectos de dosel, Perfecto y colaboradores (1997) encontraron que la diversidad en ciertos cafetales es tan alta como en los bosques tropicales conservados; tendencia que se ha encontrado también para aves, mamíferos, plantas y otros organismos (resumen en Perfecto & Ambrecht 2003; Perfecto et al. 2007; Manson et al. 2008).

Sin embargo, al igual que en la mayoría de los agroecosistemas del mundo, el manejo diversificado del café ha venido siendo reemplazado por variantes cada vez más industrializadas y menos biodiversas (Apéndice IV). En la Figura 1 se muestra la clasificación que hace más de 20 años realizaron Moguel y Toledo (1999) de los sistemas de producción de café en México, y que continúa vigente hasta la fecha. Ésta consiste en un gradiente de industrialización con un manejo que llaman tradicional o rústico en uno de los extremos, que involucra únicamente la sustitución del sotobosque por plantas de café, dejando inalterado todo el estrato arbóreo original. Después están los llamados policultivos comerciales en los cuales se reemplazan algunos árboles por especies comerciales como árboles frutales. El proceso continúa simplificando el estrato arbóreo hasta llegar a los monocultivos de sombra, donde únicamente se usa un tipo de árbol para dar sombra al café. En el extremo final del gradiente están los cafetales a cielo abierto, donde no existe estrato arbóreo. Como en otros agroecosistemas, esta simplificación en la biodiversidad generalmente va acompañada de una creciente dependencia hacia insumos externos.

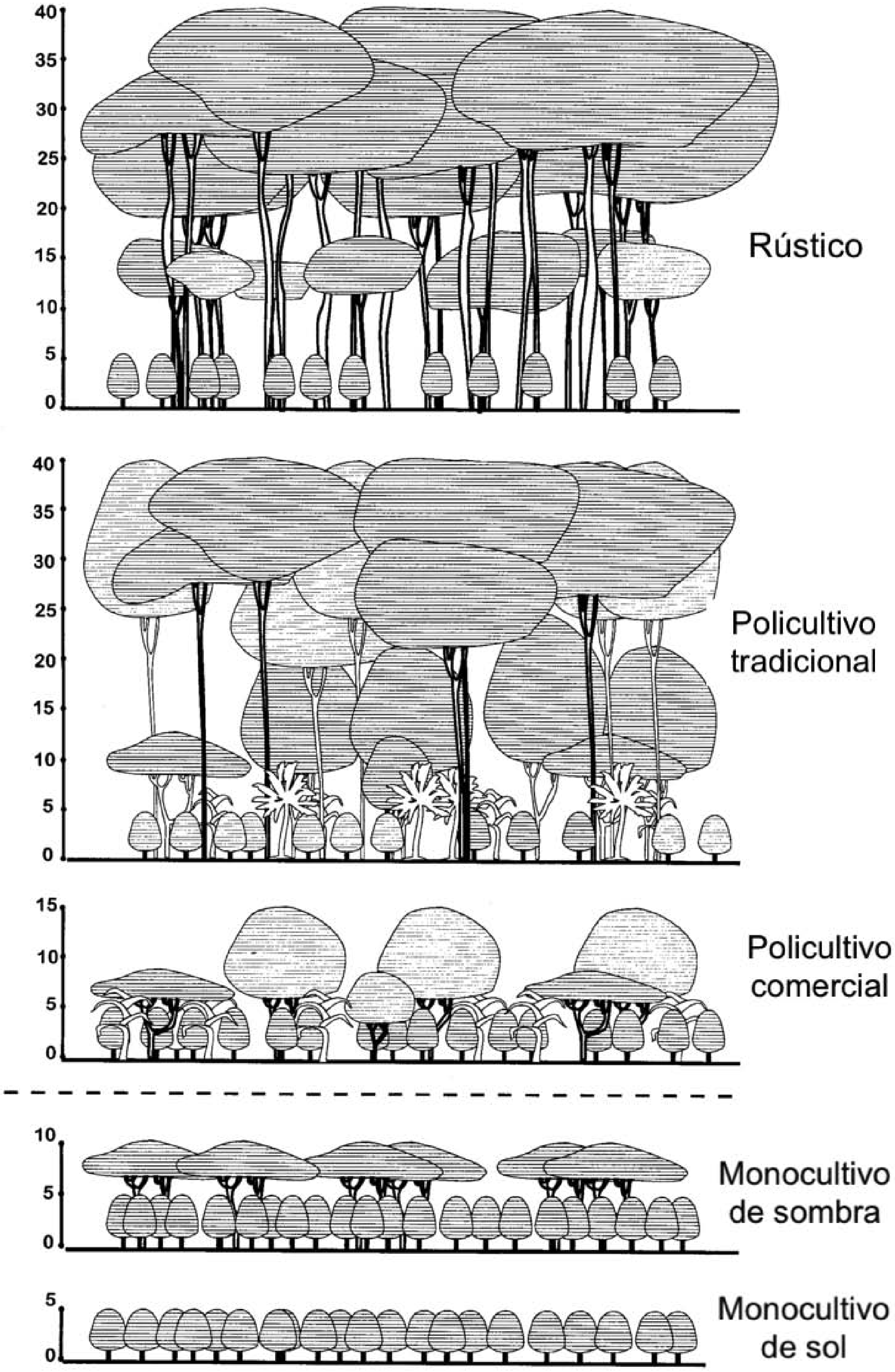

Figura 1. Clasificación de los tipos de manejo del cafetal, de menos (arriba) a más industrializado (abajo). Tomado y modificado de Moguel y Toledo (1999).

En contraste con la alta biodiversidad encontrada en los cafetales tradicionales y los policultivos comerciales, en los cafetales altamente industrializados se ha reportado una reducción drástica en la biodiversidad de aves, insectos, reptiles, mamíferos y otros organismos (Perfecto et al. 1996; Perfecto & Vandermeer 2015; Greenberg 1997; Philpott et al. 2008). Debido a que la industrialización del cafetal implica la reducción de los árboles en la plantación, la disminución de la diversidad de especies arbóreas es predecible, sin embargo, también se ha documentado una fuerte disminución de especies de artrópodos asociadas al suelo y otras partes del agroecosistema (Armbrecht et al. 2004). Poco se sabe de los cambios en las interacciones ecológicas asociadas a esta pérdida de biodiversidad, sin embargo los estudios existentes sugieren que más allá de la cantidad de sombra en un cafetal, su arreglo espacial, la identidad de las especies que la aportan y la compleja red de interacciones que mantienen es esencial para determinar la biodiversidad que será capaz de albergar el agroecosistema (Perfecto et al. 2009). Para entender mejor esto último, detallaremos a continuación algunas de las principales especies involucradas en lo que se ha llamado un sistema autónomo de regulación de plagas en el cafetal.

Figura 2. Arriba: Finca Irlanda (fotos obtenidas de Google Maps, 2020). Abajo: frontera entre la Finca Irlanda a la derecha y la Finca Hamburgo a la izquierda (foto por la autora), ubicadas en la región del Soconusco en Chiapas, México.

La red de interacciones se caracterizó empíricamente en la Finca Irlanda (Figura 2), una finca cafetalera orgánica de 320 ha situada en la zona montañosa del Soconusco, Chiapas (158110 N, 928200 W; 900 msnm), donde un grupo de investigación lleva más de 20 años estudiando las diferentes especies que viven ahí y las interacciones que mantienen entre sí (Perfecto & Vandermeer 2015). Es una región donde llueve 4500 mm/año y la vegetación original es selva media. Sin embargo, las plantaciones cafetaleras en la zona han reemplazado casi por completo la vegetación original, aunque muchas fincas aún contienen pequeños fragmentos de selva. Según la clasificación antes mencionada (Moguel y Toledo 1999), en la región existen fincas con manejo rústico, policultivo comercial o monocultivo de sombra. La Finca Irlanda tiene un manejo rústico en combinación con policultivo comercial en restauración hacia rústico, además de cerca de 50 ha de reserva de selva. En la Finca se ha reportado una alta biodiversidad de árboles, epífitas, aves, mamíferos, reptiles y artrópodos, entre otros grupos taxonómicos. Por todas estas características, se puede considerar una zona altamente conservada donde la comunidad biótica es diversa. En contraste, la finca contigua, Finca Hamburgo, es un monocultivo de sombra intensivo en el cual se utilizan únicamente árboles del género *Inga* para dar una sombra no muy densa (Mas y Dietsch 2004) y donde la aplicación de agroquímicos es común.

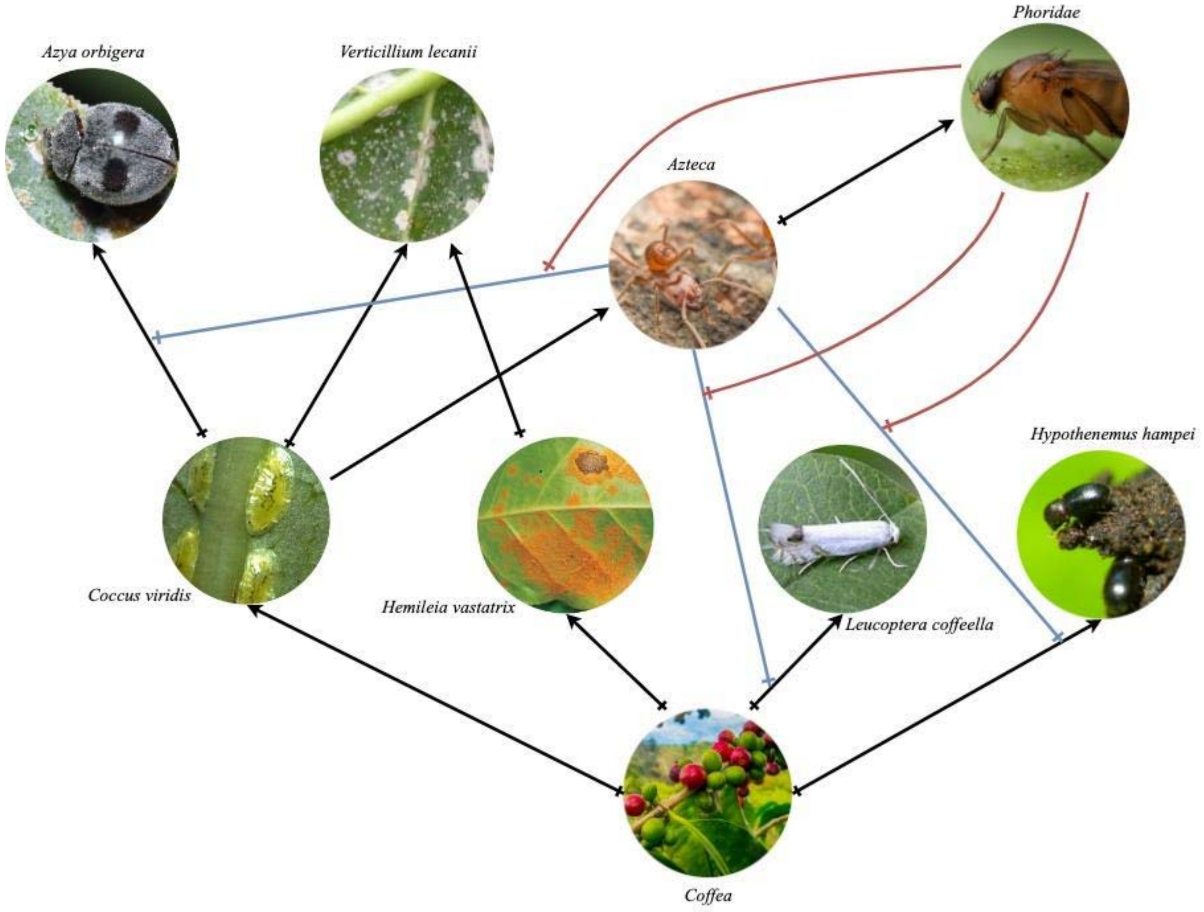

Figura 3. Algunos de los principales componentes de la comunidad estudiada en los cafetales de la región. Se muestran las interacciones de primer orden en negro, segundo orden en azul y tercer orden en naranja. Los extremos de las líneas representan el efecto positivo (flecha), negativo (línea cruzada) o nulo (sin terminación) que la interacción causa sobre el nodo en cuestión.

En la Figura 3 se muestran, de abajo hacia arriba, el café *(Coffea)* y cuatro de sus principales antagonistas: la escama verde (*Coccus viridis),* la roya (*Hemileia vastatrix)*, el minador del café (*Leucoptera coffeella) y* la broca del café (*Hypothenemus hampei)*. Las líneas negras representan interacciones de primer orden entre estos nodos y sus extremos representan el efecto positivo (flecha), negativo (línea cruzada) o nulo (sin terminación) que causan sobre la especie en cuestión. Más arriba vemos al coccinélido (*Azya orbigera)* y al hongo del halo blanco (*Verticillium lecanii)* que depredan a *C. viridis* (líneas negras). Ahora, *C. viridis* mantiene un mutualismo con las hormigas del género *Azteca,* en el cual las hormigas se alimentan de los polisacáridos que las escamas producen (línea negra), y "a cambio" las protegen de ser depredadas por el coccinélido *Azya orbigera* al patrullar la planta de café donde las escamas se encuentran y atacar a cualquier otro organismo que intente forrajear en ellas. Así, *Azteca* mantiene una interacción de segundo orden al inhibir la interacción de depredación entre *C. viridis* y *A. orbigera* (línea azul hacia línea negra). Es destacable que *Azteca* generalmente no mata a *A. orbigera*, sino que se limita a tomar los individuos y arrojarlos al suelo. Es por eso una interacción de segundo orden, pues modula una interacción de primer orden sin necesidad de alterar la densidad poblacional de *A. orbigera*. Debido a esta protección por parte de *Azteca*, las escamas alcanzan densidades poblacionales altas que aumentan su probabilidad de ser infectadas por *Verticillium lecanii*, el cual a su vez infecta al hongo de la roya (líneas negras). *Azteca*, al patrullar las plantas de café donde se alimenta de la escama verde también evita que otros herbívoros, entre ellos la broca y el minador del café, se establezcan en ellas (líneas azules). Sin embargo, las moscas de la familia *Phoridae* son parasitoides que ovipositan en las hormigas *Azteca* (línea negra), causando con su presencia que éstas se paralicen o ingresen a su nido, pausando la protección que brindan a la escama verde y a la planta del café (líneas rojas). Es en estos momentos cuando *A. orbigera* y el resto de los herbívoros pueden aprovechar para completar fases de su ciclo de vida en las plantas de café protegidas por *Azteca*. Por ejemplo, *A. orbigera* oviposita bajo las escamas, de modo que sus larvas al eclosionar se pueden alimentar de ellas, disfrutando de una densidad de alimento muy alta gracias a la protección de *Azteca* y sin necesidad de preocuparse por la misma, pues las larvas cuentan con largos tricomas que las protegen del ataque de las hormigas. Así pues, las interacciones de alto orden que *Azteca* realiza por un lado inhiben la herbivoría que algunos insectos hacen sobre el café, y por otro, causan grandes tamaños poblacionales de escama en las plantas. Estas escamas también son herbívoras del café, pero necesitan alcanzar cantidades extremadamente altas para considerarse plaga. Generalmente, antes de que esto ocurra, la densidad de escamas que genera la presencia de *Azteca* hace que las infecte el hongo del halo blanco, que por su parte es capaz de atacar a la roya, una de las plagas más importantes del café. Finalmente, las interacciones de tercer orden que mantiene *Phoridae* permite que los herbívoros que *Azteca* perjudica logren completar sus requerimientos ecológicos y se establezcan en otras partes de los cafetales (Vandermeer & Perfecto 2015 y referencias ahí contenidas).

Lo anterior es solo una fracción de las especies e interacciones que se pueden encontrar sobre una planta de café, pero es suficiente para ilustrar la enorme importancia que las interacciones de alto orden pueden tener sobre el funcionamiento del sistema y potencialmente sobre aspectos de manejo de plagas como la roya o la broca del café. Así pues, con esta información disponible, nos dispusimos a poner a prueba el papel de las interacciones de alto orden en esta comunidad mediante dos métodos de modelación complementarios: el análisis de la estructura y robustez de su red ecológica, y el análisis dinámico de sus densidades poblaciones.

c. Organización del manuscrito

Esta tesis es un esfuerzo por integrar y generar información sobre el papel de las interacciones de alto orden en la estructura y el funcionamiento de las comunidades biológicas. En el ***Capítulo I*** presentamos un artículo de revisión del estado del arte de los estudios que buscan esbozar la relación entre distintas características estructurales de las comunidades y su funcionamiento, medido de diversas formas. Aquí se hace un énfasis en aquellos estudios que abordan el tema desde el empleo de redes ecológicas, una metodología que ha resultado ser particularmente productiva en este campo. En el ***Capítulo II*** se presenta un artículo que incluye la red de un agroecosistema cafetalero particular, obtenida a través de la revisión e integración de literatura preexistente. Con esta red se realizó un análisis de robustez medida de dos maneras: a través de un índice común en la literatura que modificamos para poder incluir las interacciones de alto orden y a través de un análisis de cascada de extinción, ambas propuestas metodológicas propias. En el ***Capítulo III*** exponemos un artículo con la modelación dinámica de la red anterior, mediante el uso de una ecuación de tipo consumidor-recurso extendida para incluir interacciones de alto orden. Con esta modelación dinámica complementamos el análisis de robustez al estudiar la supervivencia de la comunidad y la abundancia de sus especies ante la pérdida de nodos y de distintos órdenes de interacción. Finalmente, se desarrollan las conclusiones generales y perspectivas de este trabajo. Además, se incluyen los Apéndices I y II que corresponden al material suplementario de cada uno de los capítulos II y III. Así mismo se incluyen los apéndices III, IV, V, VI y VII que corresponden a otros trabajos publicados a lo largo del doctorado y relacionados con la interacción agricultura-biodiversidad en distintas escalas y sistemas.

CAPÍTULO I

REVISIÓN SOBRE LA APORTACIÓN DE LOS MODELOS DE REDES PARA EL ANÁLISIS DE LAS RELACIONES ENTRE LA ESTRUCTURA Y EL FUNCIONAMIENTO DE LOS SISTEMAS ECOLÓGICOS

PREFACIO

Evaluar el estado de los ecosistemas es una labor difícil desde su definición: ¿en función de qué se evalúa?, ¿con qué sistema de valores consideramos bueno o malo su funcionamiento?, ¿con qué variables lo medimos? y ¿quién toma estas decisiones?, son todas preguntas para las cuales no hay una única respuesta. Sin embargo, dado que los ecosistemas son la base material de la cual depende nuestra existencia, y sobre todo ante la indiscutible degradación a la que los hemos sometido, nadie duda que es necesario evaluar su funcionamiento y entender aquellas fuerzas que los moldean. Para eso se ha construido una gran variedad de marcos teóricos y metodologías desde muchas ramas del conocimiento.

Dentro de la Ecología, una línea de investigación que ha sido particularmente productiva es la que emplea redes matemáticas para la representación y evaluación del estado de las comunidades (Landi et al. 2018). Ésta ha permitido definir cuantitativamente una serie de características estructurales, es decir, de la manera en que están interconectadas las especies, y después medir su impacto en una serie de aspectos funcionales como la supervivencia, la diversidad o la robustez (ésta última se ha definido de diferentes maneras, pero suele referirse a la cantidad de perturbación que un sistema puede soportar antes de cambiar a un estado diferente (Loreau et al. 2002)). Sin embargo, a pesar de lo mucho que se ha avanzado en este sentido, el trayecto ha estado lleno de resultados contradictorios. Por ejemplo, mientras que algunos estudios encuentran que a mayor conectancia (la proporción de interacciones realizadas del total de interacciones posibles), hay una mayor probabilidad de que las especies sobrevivan; otros encuentran lo opuesto (Allesina & Tang 2012; Fowler 2009). Para entender la razón de estas discrepancias, entre otras cosas, es importante sistematizar los resultados, las variables medidas, las definiciones usadas y entender los supuestos utilizados por los distintos estudios.

En este capítulo nos dimos a la tarea de revisar el desarrollo que ha habido en las principales aproximaciones metodológicas que investigan la relación entre la estructura y el funcionamiento de las comunidades, centrándonos en aquellas que utilizan las redes matemáticas como base. Revisamos los conceptos que se han utilizado y sus diferentes definiciones, y tratamos de sistematizar los resultados que se han encontrado para cada uno de ellos. En general, encontramos que para casi toda afirmación que trata de generalizar la relación, sea positiva o negativa, entre alguna característica estructural de las redes y alguna definición de su funcionamiento, existe algún estudio que la contradice. Tras analizar las posibles causas de esta falta de consenso, detallamos los avances más novedosos en los estudios de redes que intentan subsanar algunas de las limitaciones más importantes de los estudios clásicos: en particular, discutimos las redes con múltiples tipos de interacción y las redes que incluyen dimensiones espaciales y/o temporales. Detallamos el tipo de preguntas que cada metodología es capaz de responder y discutimos los beneficios de adoptar técnicas que integran una visión más amplia de las comunidades biológicas. Parafraseando a Richar Levins (2015), sostenemos que cuando dos explicaciones son válidas pero llegan a conclusiones opuestas, necesitamos plantear las preguntas de manera más amplia.

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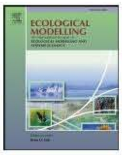

Evolution of the concept of ecological integrity and its study through networks

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A R T I C L E I N F O

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Ecological integrity
Ecological networks
Multiple interaction networks
High order interactions

A B S T R A C T

Evaluating the state of ecosystems is a major concern for humanity. For that purpose, the concept of ecological integrity has been present in both public policy and academia for decades. Here, the concept is reviewed from its origin as an ambiguous notion, through the main discourses and concepts associated with it over time and its main critiques. It is shown that a shift towards complexity sciences has permeated the study of ecosystems functioning over the last years and two main pathways have been taken: network theory and information theory, and that the concept of integrity has been gradually replaced by more transparent terms. Focusing on network theory, I first review developments in single interaction networks and find that a lack of consensus has characterized results in this area, partly due to the restrictions of these methodologies. Then I review recent advances in networks that allow for multiple types of interactions and spatiotemporal scales, highlighting the kind of insights that can be gained from each methodology and the questions ahead. Implementing these new frameworks will likely continue to bring novel insights into the functioning of ecosystems and how different management strategies contribute to it.

1. Introduction: assessing ecological integrity

The word integrity was first used in the context of ecology by the famous environmentalist Aldo Leopold in 1949 (Leopold 1949) and it has been present in public policy at an international level since its appearance in the 1972 U.S. Clean Water Act (Barbour et al., 2000). Soon after, Karr and coworkers defined it for the first time as “the ability to support and maintain a balanced, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitats within a region” and started using it to evaluate aquatic environments (Karr 1981; Karr and Dudley 1981). They also said that it is the ability to withstand and recover from perturbations, ideas that are now embedded in the concepts of resistance and resilience (Andreasen et al., 2001). According to Manuel-Navarrete and coworkers (2004) the main discourses around integrity have evolved as follows: i) Early conceptualizations of integrity considered it as a measure of pristineness, as a state of the environment when humans are absent, that can be measured empirically and objectively. These ideas prevailed during the seventies and eighties. ii) In the nineties, ecosystems started to be thought of as dynamic systems whose integrity falls in their ability to deal with perturbations. Attention shifted from elements to processes, but the existence of an objective ideal state was still present, and it was still supposed to be measured independently of social values. iii) Later, complex systems theory permeated integrity conceptions, along with the notion of alternate equilibriums. The role of science became providing information on how different ecological regimes could be pursued and their compatibility with socially dictated values was now acknowledged as an important factor for determining integrity (Manuel-Navarrete et al., 2004). Nevertheless, these ideas have not replaced each other, rather they coexist, and it is not uncommon to find elements from the three of them in a single paper.

In this review I ask how integrity is measured according to the three main discourses around it. I show how concepts like **resilience, robustness, stability, sustainability** (see Glossary) and others have been historically linked to integrity, as they have been explicitly or implicitly regarded as proxies for it, as a part of it, or even used as synonyms for it. I refrain from aligning myself with a particular definition of integrity, as my goal is for the reader to know that its definition is changing, and to understand the different meanings and implications it has had. Nevertheless, I align with those authors who consider a better choice to use these last concepts alone, without obscuring them with the use of integrity and the sense of morality it entails (Marris and Rohwer

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2022). I focus on the complexity-based approach to these concepts. Particularly, the analysis of ecological networks has brought major insights in the way ecological communities are structured and how this affects their dynamics. This is why I include research that does not necessarily claim to measure integrity but deals with some of the mentioned concepts and with structure-dynamic relationships. I review the principal insights that the study of **single interaction networks** has brought on how structure and dynamics of ecosystems influence each other; and then I review the more recent advances on **multiple interaction networks** and **adaptive networks**, to show how they promise to expand our understanding of the mechanisms that shape ecological systems.

2. The very changing definitions of ecological integrity

2.1. Origins: the healthy ecosystems

Most research traces the concept of ecological integrity to Aldo Leopold, whose ideas on environmental ethics greatly influenced the movement for wildlife conservation in the U.S. (Barillas 1996; Betancourt 2014). It was in his essay *The Land Ethic* that he wrote "A thing is right when it tends to preserve the integrity, stability, and beauty of the biotic community. It is wrong when it tends otherwise" (Leopold 1949). He did not define the concept, but Leopold's thinking had a major influence on environmental public policy and by 1972 the Clean Water Act -which is the federal law that governs water pollution in the U.S.- mentioned integrity in its primary goal: "restore and maintain the chemical, physical, and biological integrity of our nation's waters". From there, it was included in many other public policy documents and in the scientific agenda, a reality that continues to this day (Karr 1993; Kim and Bosselmann 2015). Nonetheless, it was until 1981 that James Karr and his co-workers gave the first formal definition in the context of aquatic environments (Karr and Dudley 1981).

During these first years, scientists focused on the development of indexes to measure integrity (Noss 1990; O'Connell et al., 1998; Karr and Chu, 1999). Karr (1981) developed the first Index of Biotic Integrity (IBI) in order to assess the quality of water resources, which was based on the richness of fish species, trophic composition and health of individuals. This index was quickly implemented in policy in the U.S and Europe (Plafkin et al., 1989; Kerans and Karr 1994), with agencies and states adapting it to their particular goals (e.g. Oberdorff and Hughes 1992). In these approaches, ecological integrity is continuously compared to an organism's health and measurements are compared to an "optimal", unperturbed condition. Evaluations should reflect the "multivariate nature of biological systems" (Karr 1993), hence, indexes are multimetric, and should be relative to expected regional conditions at various scales. As such, they are aimed to detect the position of an ecosystem along a gradient of degradation and help identify the factors responsible for it.

Even though Karr himself advised caution about the adherence to a strict human health metaphor, noting that biological assemblages are not precise analogues of mammalian bodies, he still called for the expansion of the health concept and the convergence of medicine and ecology on ecological integrity. Mixed with formal definitions, these researchers too often included ambiguous notions, for example, that systems have integrity when their inherent potential is realized, and its condition is stable, complete, or undivided (Karr 1993). These concepts were commonly mixed with an ethical view of nature conservation in which integrity was deemed as an indicator of goodness in ecosystems (Lemons and Westra 1995). This ethical view of nature, since the eighteenth century, through Leopold and well into contemporary conservationism, has too often been used to justify the exclusion of local residents from their lands, mainly Native Americans and Black people, in order to protect an ideally pristine wilderness (Dowie 2011; Sarkar 2021).

Andreasen et al. (2001) discuss the optimal condition that serves as point of comparison for integrity indexes. According to them, the optimum condition is that in which *naturalness* is present, but they define naturalness as "something of great esthetic and spiritual importance", a quality that should be measured in relation to what would have happened in America if the European settlers had not interfered. As in all studies following this discourse, an artificial dichotomy between human and nature is present in the idealization of pristineness, a notion that has permeated American environmentalism since its origins and which is deeply plagued with racist and colonial biases (Sarkar 2021). This integrity discourse continues to be used and it is materialized, for example, in the natural parks system in the U.S. where a pristine nucleus is assumed to represent the optimal condition, buffer areas are sought to be kept healthy and the rest is regarded merely as a human-polluted area (Woodley 1990; Parks Canada 2001). Its measurement relies on experts who are supposed to determine integrity empirically through indicators and inform legislators, who in turn execute commands to maintain it (Manuel-Navarrete et al., 2004).

2.2. Systemic approaches

Beginning in the nineties, integrity discourses started to emphasize the dynamic nature of ecosystems, and attention was put in their ability to self-organize. In this discourse, integrity lies in the systems' capacity to deal with perturbations, so the concepts of resilience and resistance are fully adopted (Kay, 1991). It is acknowledged that all ecosystems are influenced by humans, so pristineness is no longer the main focus. There is still an assumption of a better overall direction for ecosystem evolution, but integrity is now about how much can they deviate from it without arriving at an irreversible change (Manuel-Navarrete et al., 2004). Holling's ideas on alternate attractors and **adaptive cycles** were very influential for this conception (Holling 2001). Disturbances are deviations from the so-called attractors, and management's goal is to keep these deviations from pushing the system into a different attractor. In this discourse, ecosystem function is more relevant than its composition, so functional groups are measured instead of species and aspects like redundancy are rendered important to attenuate the effects of species loss. Research focuses on processes, not elements. Resilience, which is generally understood as "the ability of a system to deal with perturbations and reorganize in the face of changes, maintaining its structure, functioning and identity" (Walker et al., 2004), is the main wanted characteristic. Nonetheless, some authors have pointed out that caution should be had when applying this concept. Mainly, resilience is understood as an intrinsically positive and desired property of ecosystems (Biggs et al., 2012), but it is generally measured from an ahistorical point of view which ignores the power relations and conflicts that influence the systems (Olsson et al., 2015; Stojanovic et al., 2016). Moreover, some critics have said that the resilience framework can be used to justify and perpetuate the *status quo*, thus maintaining unequal power relations. In order to avoid this, resilience studies should specify what it is that we are seeking to maintain, for whom, and in the face of what (Walker and Cooper 2011; Cretney 2014; Cretney and Bond 2014). This caution, however, is lacking in the integrity analyses that fall into this discourse. In these studies, the ethical imperative of preserving nature remains present, and it is presumed to be objective instead of recognizing the interests behind of what is trying to be preserved. This is reflected in the fact that even though management is now supposed to be adaptive, meaning that it should evolve in the face of the social and ecological changes, these changes are rendered inevitable and implementation schemes are done through top-down policy making. Ecological integrity is still deemed as an objective state that can be determined by scientific experts by understanding structural relations.

This discourse was broadly adopted in North America (Born and Sonzogni 1995). For example, Parrish et al. (2003) outline a way to measure ecological integrity that has been used within protected areas. This consists of selecting target taxa, then identifying ecological attributes that are key for them and defining an acceptable range of variation for these attributes. The status of each target is rated through an assessment of the state of their ecological attributes and they are combined into an overall measure of the whole area. The ecological attributes are the focus of management, not the species themselves. Instead of being compared with an optimum value, they are allowed to vary inside an acceptable range which is obtained from sources like ecological models, expert knowledge, and comparisons with similar systems and among gradients of disturbance.

With the adoption of Holling's ideas, ecological integrity entered the realm of the complexity sciences, and the consolidation of these ideas along with the recognition of social values gave birth to a third discourse (Manuel-Navarrete et al., 2004). In it, the role of science shifts from discovering an objectively better state of ecosystems to facilitating negotiation among conflicting values. The possibility of different ecological regimes to have integrity is recognized and science's job is no longer to decide which one is correct, but to say what the different ecological regimes look like and the trade-offs involved in management actions. Integrity in this discourse is determined by the states that are both biophysically possible and compatible with the needs of a society characterized by diverse and often conflicting values. Methods overall are the same as before, but they incorporate uncertainty and the fact that the criteria by which one makes decisions are subjective.

Examples of this conceptualization is the ecosystem-based management which has been applied, for example, in the Great Lakes Basin of the U.S. (Konisky and Beierle 2001), and the Environmental Integrated Management (Born and Sonzogni 1995). Another example is collaborative management, in which stakeholder's values are considered dynamical and an emphasis is made on the process of learning, so their opinions on management can change and common interests can be discovered (Saarikoski 2000; Allen et al., 2001). Several limitations to this approach have been pointed out, for example, that different social actors usually come from different positions of power, so weighing their interests on an equal basis can result in an artificial sense of justice that overshadows political differences and historical debts (Luke 2002). Instead, the interests of local and historically marginalized actors should be prioritized, as they are the first affected by environmental management strategies. Indeed, it has been shown that the demands of local social movements have historically been at the front of many environmental causes, with academia and public institutions summing up later, so listening to the demands of people and providing them with social learning spaces and tools for capacity building can be a better management strategy (Stirling 2019). In an example of this last approach, some groups have developed games that are based on a system's driving processes. For example, the ecological network associated with a coffee agroecosystem, which involves direct and trait-mediated interactions that shape an autonomous pest control system, was translated into a board game that enables peasants to reflect on the role of biodiversity in their systems (García-Barrios *et al.* 2016). On another example, farmers that share the irrigation systems of the Senegal River Valley used a role-playing game in order to discuss different strategies of co-ordination amongst themselves (Barreteau et al., 2003). Through playing, local social actors can grasp the complex dynamics of a biological system and to analyze the implications of different management decisions, which they can then take into their hands (see also García-Barrios et al. (2008), Speelman et al. (2014), García-Barrios et al. (2015), and Speelman and García-Barrios, (2006) for more examples on the use of games for promoting learning and decision making in various socio-ecological systems).

2.3. Novel approaches from a complexity viewpoint

Mainly in the last decade, complexity-based approaches to integrity have thrived along two pathways, namely, network theory and information theory (Equihua et al., 2020). While both approaches aim to understand the function of complex phenomena through the use of mathematical formalisms, network theory does it by analyzing the structure of connected entities, while information theory looks in the response variables of a system for activity patterns. I will briefly describe the main proposals of the information theory approach and then focus on network-based analyses. Even though I present the most recent advances in methodological terms, most of them fall into the second discourse of integrity. This is, approaches with a systemic view of biological assemblages that use tools from complexity theory, but that lack the incorporation of explicit social values and power relations.

Equihua et al. (2020) review and propose information theory as a unifying framework to understand ecological integrity and resilience, which they treat as different but linked concepts. For them, integrity is defined by the particular structure and functions of ecosystems, and resilience is their ability to preserve them in the face of perturbations. For Equihua and co-workers, integrity arises from processes of self-organization derived from thermodynamic mechanisms that operate through the existing biota, as well as the energy and materials at their disposal, until attaining optimal operational points which vary according to changes in the biophysical conditions (Equihua et al., 2014; Equihua et al., 2020). They point out the main approaches for assessing integrity with information theory.

The first one is through the concept of ascendancy, a measure of information flow (Gustavson et al., 2002). Saint-Béat et al. (2015) explain that to understand ascendancy, two kinds of stability must be differentiated. A system with high inner stability has inner constraints typical of an organized structure, which results in high ascendancy. On the other hand, low ascendancy is linked to redundancy, which makes ecosystems resilient to external disturbances. Too little ascendancy is interpreted as a lack of internal constraints, whereas too much of it makes them inflexible and vulnerable to external perturbations; so ecosystems should have intermediate ascendancy levels.

A second approach to integrity returns to the concepts of ecosystem health and stability.Ramírez-Carrillo and collaborators (2018) propose an ecosystem health index based on the notion of criticality, which they define as a balance between order and disorder in the fluctuations of the system's state variables. According to these authors, healthy ecosystems have state variables, like respiration, whose fluctuations are characterized by pink noise, which happens when fluctuation autocorrelation is intermediate between zero (which they associate to the system's **adaptability**) and high values (which they associate with robustness). Several authors have found evidence of this criticality in physiological processes such as heart activity, and they have associated it with a healthy state (Ivanov et al., 1996; Rivera et al., 2016). However exciting this line of research may be, we should be cautious about the analogy between human and ecosystem health. A strict analogy would require the existence of an unequivocally optimum condition for ecosystems and homeostatic processes that maintain it. Even though there may be mechanisms that enable ecosystems to be disturbed without profound structural or functional changes, they are fundamentally different from homeostatic processes because the components of ecosystems do not function as a co-dependent unit like organs in a body do. Ecosystems may change, but they do not die altogether (Wicklum and Davies 1995). In this sense, monitoring variables such as ecosystem respiration certainly gives information on the ecosystem's state but is not equivalent to monitoring vital signs in an organism and hence they cannot be used to objectively call an ecosystem's state "good" or "bad".

Finally, Cabezas et al. (2005) proposed the Fisher information index to measure variation and order as conditions relevant for sustainability (for further developments of this idea see Ahmad et al. (2016)). Very ordered systems have a Fisher information that tends to zero, while disordered systems have a high Fisher information. The thesis proposed by Frieden and Gatenby (2010) is that systems in stable dynamic states have constant Fisher information, while changes in it can signal regime changes. Their results are consistent with Michaelian (2005) ideas about ecosystem stability and entropy, where stable ecosystems have higher values of entropy.

As we can see, information theory approaches to integrity have focused on the balance between order and disorder (Fisher information and criticality approaches) or constraint and flexibility (ascendancy approach). They are phenomenological approaches, since they do not seek to find out the mechanisms behind the state variables that are measured. These methodologies benefit from the huge amounts of data on ecological phenomena that are now available. A major challenge to these developments is to distinguish quality from quantity in their choice of data and to be cautious as to the applicability of their analogies and assumptions.

3. Ecological networks

The study of ecological assemblages with network theory has brought a great number of insights about the processes governing them. The multiplicity of contexts in which networks have been applied, just in the science of ecology, is outstanding. Of course, all these developments have not been without controversy, as the search of general relations between structure and function of networks has often given contradicting results. Here, I will start by reviewing the major topics and results brought on by the study of single interaction networks, and then move on to more recent proposals involving adaptive networks, spatially distributed networks and multiple interaction networks. Most of these studies do not refer explicitly to ecological integrity, but they all measure relationships between structure and function of ecosystems, and use resilience, stability, robustness and other better-defined concepts that have been related to ecological integrity. I will focus on the kind of insights that have been gained with each methodological approach and how they contribute to our knowledge of the state of ecosystems.

3.1. Single interaction networks

The majority of research on network theory has focused on networks composed of nodes representing species or functional groups and which are connected by a single type of ecological interaction, mainly antagonic (e.g. herbivory, predation, parasitism), mutualistic (e.g. pollination) or competitive. Landi and collaborators (2018) reviewed publications on these three types of networks and synthesized their main questions and findings. Overall, these studies focus on finding the relationships between some structural characteristics of the networks and their function, measured as robustness, stability, resilience and other concepts that were discussed in earlier sections. Generally, there is a lack of consensus in many of the relationships that have been studied, which is probably due to methodological differences and working definitions, in addition to the intrinsic complexity that stems from the numerous elements, processes and scales that interact to give rise to these qualities (Ives and Carpenter 2007).

The main structural characteristics that have been measured are **species richness, connectance, weighted connectance, connectivity, linkage density, weighted linkage density, species strength, species dependance, modularity** and **nestedness**. These features have usually been studied as independent variables, and the corresponding dependent variables have been **linear stability, resilience, persistence, structural stability, extinction cascade, robustness**, and **invasibility**. In the most simplified way to put it, the overall question asked has been if these independent variables have a positive or a negative effect on the dependent variables, but different answers have often been provided by researchers using different methodologies, both empirical and theoretical. For a comprehensive review on the impacts of structural properties on network function see Landi and collaborators (2018). Here, I will summarize the main findings in order to show the overwhelming diversity of answers that have been given to this question and how they vary depending on the type of network used (trophic, mutualistic or competitive) and general methodology.

3.1.1. Species richness

Early ideas on the topic mainly said that enhanced diversity made ecosystems stable through species limiting each other's growth, through predation or competition, thus preventing destabilizing outbreaks (Odum 1953; MacArthur 1955; Elton 2020). These notions remained unchallenged until the now classic work of Robert May (1972). Using linear stability analyses, he showed that communities modelled as random networks lose stability as the number of species, the number of interactions, or their strength rise. These results have been causing controversy for decades, as they seem counterintuitive in the face of the staggering biodiversity of some of the world's ecosystems.

The work of May conveyed all interaction types, as the sign of the elements in the community matrix could be positive or negative. Since then, researchers have tackled the issue mostly with single interaction networks and the result has been a general lack of consensus. For example, in networks defined by predation or competition, richness has been found to have both a positive and a negative effect on integrity-related concepts like stability, robustness, productivity, invasibility, feasibility, coexistance and diversity (Pimm 1979; Lawlor 1980; Pimm 1980; Tilman and Downing 1994; Tilman, 1999; Borrvall et al., 2000; Dunne et al., 2002a; Christianou and Kokkoris, 2008; Dunne and Williams 2009; Fowler 2009; Gross et al., 2009; Maynard et al., 2017; Zhao et al., 2019; Maureaud et al., 2020). On the other hand, in mutualistic communities, there has been more consensus around a positive relationship between species richness and both resilience and persistence (Okuyama and Holland 2008; Thebault & Fontaine 2010; Vidal et al., 2020).

3.1.2. Connectance and connectivity

There is also widespread controversy around the relationship between connectance and community function, with many studies supporting both positive and negative relationships, depending on the methods used to generate theoretical networks or the particular empirical dataset (Landi et al. 2018). For food webs and competition networks, connectance and connectivity have been found to have a positive effect on stability (Haydon 2000; Fowler 2009; Van Altena et al. 2016; Baumgartner 2020), while in mutualistic webs they have had both positive and negative effects on local stability, propagation of perturbations, extinction cascades, persistence and resilience (Okuyama and Holland 2008; Thebault & Fontaine 2010; Allesina and Tang 2012; James et al., 2012; Suweis et al., 2015; Vieira and Almeida-Neto 2015).

3.1.3. Degree distribution

The degree distribution of networks has been associated with their capacity to persist, and different distributions have been found to characterize different types of networks. Food webs have a degree distribution that differs from a Poisson, which is typical of random webs. Aside from that, the specific distributions associated with food webs have been highly controversial and different authors have found different fits. For example, the exponential distribution has been commonly found (Camacho et al., 2002; Dunne et al., 2002b); a uniform distribution has also been associated with webs with high connectance; and power-law and truncated power-law distributions have been found for communities with very low connectance (Dunne et al. 2002b; Montoya & Sole 2002).

In mutualistic networks, a major interest has been the proportion of generalists against specialists. Jordano et al. (2003) found truncated power-laws, which is in agreement with the idea that mutualistic webs have a high prevalence of specialists and rare super-generalists. Okuyama (2008) found a gamma distribution. The impact of degree distribution on network function is also debated, as Feng and Takemoto (2014) found that heterogeneity in node degree distribution negatively affects their local stability, while James et al. (2012) found that individual node degrees are good predictors of species survival.

3.1.4. Strength of interactions

Working with weighted interactions has brought a lot of new insights to our knowledge of ecological networks. Variability in link strength has been found to be related with trophic network stability, and it has been commonly observed in empirical networks (Berlow et al., 2004; Wootton and Emmerson 2005). In particular, the existence of many weak interactions and few strong ones appears to promote stability by dampening oscillations or reducing the amount of intraspecific competition needed for stability (McCann et al., 1998; Neutel et al., 2002; Thebault & Fontaine 2010; Van Altena et al. 2016). Emmerson and Yearsley (2004) supported these findings, but only when omnivory is present. In contrast, Allesina and Pascual (2008) found that stability is robust to changes in the strength of the Jacobian elements. Further, Allesina and Tang (2012) showed that a preponderance of weak interactions decreases the probability of communities to be stable, a result previously found with different methods by Borrvall et al. (2000). A different approximation has been the use of bioenergetic models, where interaction strengths are parameterized according to body mass ratios. Emmerson & Raffaelli (2004) and Otto et al. (2007) show that such scaling promotes stability in food webs.

Considered together with trophic interactions, it is recognized that adding intraspecific competition (negative terms on the diagonal of the interaction or community matrix) increases stability (Haydon 1994). Furthermore, De Angelis (1975) found that a bias towards strong self-regulation of the species at higher trophic levels stabilizes food webs. Haydon (2000) showed that a high connectance between highly and weakly self-regulated components is required.

In mutualistic networks, the strength of interactions is often inferred by the relative number of visits of pollinators to the plant. Doing so, Jordano (1987) and Bascompte et al. (2006) found an even stronger skewness towards weak interactions. The last one also found that while animals depend strongly on the plants, plants rely poorly on their animal pollinators or seed dispersers (Bascompte et al., 2006), concluding that both heterogeneity in interaction strength distribution and asymmetry of species dependences facilitate the maintenance of biodiversity. The ability of the system to reduce the propagation of perturbations had been linked to connectance as shown above, but Suweis et al. (2015) found that heterogeneity in interaction strength distribution also contributes to it. Even though most studies agree on this issue, there have been exceptions who have found the opposite relationships (Okuyama and Holland 2008; Feng and Takemoto 2014). Also, Rohr et al. (2014) showed that the distribution of interaction strength had no impact on structural stability and that it was an average high strength that mattered.

3.1.5. Modularity and nestedness

It has almost been accepted that food webs have a more modular structure than other types of networks and that this is related to their stability. Along with a weakly connected arquitecture, many studies reported that modularity increased the stability or the persistence of food webs (Moore and Hunt 1988; Ives et al., 2000; Krause et al., 2003; Thebault & Fontaine 2010; Stouffer and Bascompte 2011). However, Grilli and collaborators (2016) used a random networks approach to show that modularity influences stability in different ways depending on other parameters like connectance, mean interaction strength, variance, correlation and size of modules.

For mutualistic networks, nestedness has proven a more important feature than modularity. While Olesen et al. (2007) and Mello et al. (2011) noticed that modularity is present in some mutualist networks, and that it tends to increase as webs get bigger; Thebault and Fontaine (2010) emphasized that its effect on persistence and resilience is negative. Nestedness, on the other hand, has been accepted as a characteristic topological feature of mutualist networks (Bascompte et al., 2003). It has been shown to prevent extinction cascades (Memmott et al., 2004), enable coexistence (Bastolla et al., 2009), increase persistence and resilience (Okuyama and Holland 2008; Thebault & Fontaine 2010), and maximize the parameter domain that leads to stable and feasible equilibriums (Rohr et al., 2014). However, this has also been refuted by some studies. For example, James et al. (2012) studied 59 empirical webs and found nestedness to be a secondary covariate to the number of mutualistic partners, which they found to be a better causal predictor enabling coexistence. Allesina and Tang (2012) found local stability to be negatively affected by nestedness and Campbell et al. (2012) showed that extreme nestedness promotes extinction cascades.

In conclusion, basically all structure-function relationships that have been studied in single interaction networks have been controversial. Aside from methodological differences, the big number of contradicting results may be because almost none of them have controlled for the influence of other types of ecological interactions, nor have they studied temporal changes in their properties. If there are generalities to be found in the relationship between the structural and functional features of ecological networks, it may be that a broader view is necessary. In the next section we will see approaches that tackle these shortcomings.

3.2. Multiple interaction networks, spatial networks and adaptive networks

It has become clear that the effects of different types of interactions need to be assessed in order to understand ecosystems (Sander et al., 2015; Soliveres et al., 2015; Golubski et al., 2016; Kéfi et al., 2016; Pilosof et al., 2017). In addition to all the structural features discussed above for single interaction networks, communities that take into account various types of interactions will probably be influenced, at least, by 1) the proportion of the different interaction types, 2) the relative strength of interactions within and among interaction types, and 3) the structural properties of each sub-network and the overall aggregated network (García-Callejas et al., 2018).

The recollection of empirical data on multiple interaction networks can be challenging, as even single interaction networks are commonly undersampled (Chacoff et al., 2012) and quantifying interaction strength requires a huge sampling effort (Berlow et al., 2004). Strategies for multiple interaction network construction have basically been aggregating data from previous work with a particular network (Kefi et al., 2015) or the design of massive sampling programs. Following this second strategy, Pocock et al. (2012) sampled different habitats in an agroecosystem in the UK, obtaining a network containing trophic, mutualistic and parasitic sub-networks. They showed that, overall, the sub-networks' robustness did not strongly covary, suggesting that restoration programs aimed at benefiting one functional group will not necessarily benefit the others. On the other hand, they found that some species were disproportionately linked to species in all sub-graphs, suggesting that a better strategy for restoration should focus on them. As for estimating interaction strength, evidence seems to support a neutral view of interactions, in which their frequency can be approximated as the result of random encounters mediated by the relative abundances of the populations involved, and their frequency can be in turn used as a proxy for their strength (Canard et al., 2012, 2014; Faust and Raes 2012; Araújo and Rozenfeld, 2014; Cazelles et al., 2016).

García-Callejas et al. (2018) reviewed developments on multiple interaction networks, which have only appeared in the last decade, and recognized three non-exclusive methodologies: **extended food webs, equal footing networks** and **multilayer networks** (see their paper for a complete list of articles published with each methodology). These are differentiated based on how different interactions are classified (either by the general positive, negative or null effect they produce on other species or by the particular mechanism by which the interaction occurs), whether they are expressed in the same units or not. These three approaches have different assumptions and are best at addressing different kinds of questions.

3.2.1. Extended food webs

Extended food webs take trophic interactions as the backbone of the community, whose dynamic is modelled through differential equations (e.g. Lotka-Volterra), but which incorporate non-trophic interactions as functional modifiers of the equation's parameters. For example, Arditi et al. (2005) built a model of mass conservation in which non-trophic positive interactions (that can be understood as mutualisms) have a positive effect on the species ability to efficiently incorporate nutrients into their biomass. Importantly, this effect of non-trophic interactions was found to be much stronger than that of species richness in the web. Arditi et al. (2005) inserted non trophic interactions as modifiers of the elements of the community matrix A_{ij}, meaning that the population density of species k modulates the trophic interaction between two other species i and j, without directly affecting the population densities of either of them. This kind of mechanism has also been called "high-order interactions" by Bairey et al. (2016) and they have been shown to promote community linear stability in random networks. They have also been documented empirically, for example, in agroecosystems. Vandermeer et al. (2010) describe an ecological network composed of the main coffee pests and their natural enemies in a diversified coffee plantation, where they find that a series of high-order interactions are essential to regulate the pest population densities, resulting in an autonomous pest control system.

More recently, Kefi et al. (2012) extended the methodology by Arditi et al. (2005) to allow for non-trophic interactions to influence any parameter of a food web dynamic model, for example, reproduction and mortality rates, migration rates, or others, according to the mechanism by which they happen. For example, the provisioning of nesting sites by some species positively affects the reproduction rate of another species, or foot stamping by big mammals can increase mortality rates of some herbs. In this way, extended food webs have the potential to include direct and indirect effects on unlimited biological detail, at the cost of an ever increasing number of parameters and larger equations.

3.2.2. *Equal footing networks*

In equal footing networks, it is assumed that all kinds of interaction mechanisms can be summarized by the positive, negative or null effect they produce in the species growth rate, so they are all aggregated in the elements of the community matrix A_{ij} instead of being modelled with auxiliary equations. Hence, the community matrix includes all possible pairwise combinations ((0,0), (0,+), (0,-), (+,0), (-,0), (+,+), (-,-), (0,0)). At the cost of losing detail about the mechanisms that produce the effect, equal footing networks gain generality and scalability, as the number of parameters does not increase so fast. This approach was used to show that local stability is enhanced by a combination of trophic and mutualistic interactions (Mougi and Kondoh 2012; Kondoh and Mougi 2015). Afterwards, they expanded their studies to show that commensalism and amensalism (Mougi, 2016a) also increase local stability.

Since equal footing networks can be modelled with the same equations as single interaction networks, and their stability can be analyzed in the same way, they are a natural opportunity to compare results with one and many types of interactions. It may still be too soon to say, but studies so far indicate that networks with many interaction types are more locally stable than their counterparts (García-Callejas et al., 2018).

3.2.3. *Multilayer networks*

Pilosof et al. (2017) formally defined multilayer networks as (1) a set of physical nodes representing entities (for example, species); (ii) a set of layers, which can include multiple aspects of layering (for example, interaction type); (iii) a set of state nodes, each of which corresponds to the state of the physical node on a specific layer; and (iv) a set of edges to connect the state nodes to each other in a pairwise fashion. The edge set includes both the familiar 'intralayer' edges and 'interlayer' ones. This idea has already been used in areas like engineering, economy or social network analysis (see Boccaletti et al., 2014 and Kivelä et al., 2014 for reviews).

For representing the dynamics of a multilayer network, state nodes in each layer can be modelled with a particular equation corresponding to one type of interaction, and auxiliary equations may connect the state of nodes of a given entity in different layers. Such inter-layer links may represent any kind of relationship between layers, which makes this approach particularly flexible, of course, this entails the difficulty of choosing how to define them. (García-Callejas et al., 2018).

The application of multilayer networks in ecology has begun to show that communities, when many kinds of interactions are considered, are highly structured (Melián et al. 2009; Kéfi et al., 2015) and that this has repercussions on different community properties (Pocock et al., 2012; Evans et al., 2013; Kéfi et al., 2016). For example, Kéfi et al. (2016) combine a multilayer and an extended food web approach (as I have said, these methodologies are non-exclusive) to analyze a marine ecosystem. They find that hundreds of nodes and links belonging to trophic, positive non-trophic and negative non-trophic interactions form a strikingly simple 3-D structure with few modules that are taxonomically coherent and easily interpreted in terms of species traits (e.g. mobile consumers, sessile habitat facilitators, competing primary producers, etc.). They also found that the structure of non-trophic interactions allow for a higher persistence and total biomass than what would be expected from their random allocation.

This approach is a powerful tool as it can provide a way to analyze the importance of different interaction types in processes such as population dynamics and properties such as resilience. It can also give a broader definition of node centrality, which can be used as a proxy for finding keystone species, that can incorporate their participation in several types of interaction (Pilosof et al., 2017).

Interestingly, the equal footing framework can be thought of as a particular type of multilayer framework in which all layers are "flattened" into a single one, erasing inter-layer links and making each node simultaneously affected by all interaction types (García-Callejas et al., 2018). Melián et al. (2009) provide an example of an equal footing model made from a multilayer dataset.

3.2.4. *Spatial and temporal variables in networks*

As the reader may already have noticed, layers in a multilayer network can not only represent different types of interaction, but also different moments in time, different spatial locations, levels of organization or group identities (Pilosof et al., 2017). For example, layers can represent patches while interlayer edges can represent species dispersal between them, or layers can represent seasons and while interlayer edges can be changes in the species' abundance. Spatially defined multilayer networks can help explore the stability of communities under different spatial patterns, and help advance metacommunity theory. These multilayer objects can be thought of as "networks of networks", where habitat patches are the nodes of a spatial network across the landscape, and each at the same time contains a local network of species interaction with each other.

Single interaction networks have already explored spatiality. For example, Bunn et al. (2000) used a focal species analysis with a graph approach to landscape connectivity in the Coastal Plain of North Carolina. They built graphs using GIS to define habitat patches and determined the functional distance between them with least-cost path modeling. Performing edge and node removals, they analyzed how species with different dispersal capacities perceived the landscape, and each patch`s role in maintaining connectivity. A similar study using the Mexican Spotted Owl can be found in Urban and Keitt (2001). These approaches have proven useful for conservation planning at a landscape scale. According to Reza and Abdullah (2011), a regional index of integrity should incorporate measures on fragmentation and landscape connectivity, among others. The use of multilayer networks promises to improve them by allowing researchers to study the impact of environmental changes, landscape and species at the same time, and recent frameworks are seeking to organize how we deal with these new tools (Fortin et al., 2021).

On the other hand, networks that change through time have been called adaptive networks, and their analysis has revealed that important structural changes take place in communities according to seasonal or successional changes (Villa-Galaviz et al. 2012; López-Carretero et al. 2014; Saavedra et al., 2017). For example, in tropical ecosystems with seasonal climatic variation, it has been shown that the specialization and structural patterns of plant-herbivore networks can dramatically change (López-Carretero et al. 2014; 2018). According to López-Carretero and collaborators (2014), selectivity and modularity of plant-herbivore networks decrease during the dry season and in poorly structured habitats, as generalist species expand their host preferences in the face of resource limitation. This increase in connectance can then reflect species ability to adapt and buffer the negative impacts of disturbance. In another study, Villa-Galaviz and collaborators (2012) studied the changes in network structure of a plant-herbivore community across successional stages of a tropical dry forest. By focusing on networks structure rather than on species identities, they found that robustness (e. g. low extinction in the face of random node removal) was quickly recovered after perturbation, as they found no significant differences in robustness-related structural measures between mature forests and middle and late successional forests.

The importance of rewiring interactions in ecological networks has just begun to be understood. While the above mentioned studies indicate that changes in interactions do result in structural changes, other studies have claimed that these have a minimal effect on network architecture (Petanidou et al., 2008; Carstensen et al., 2016; Trøjelsgaard and Olesen 2016). However, Saavedra et al. (2017) demonstrated that network reorganization can play an important role in modulating succession, even when global structural properties remain invariable. In an interesting fusion of empirical and theoretical analyses, they use a Lotka-Volterra competition model calibrated through field observations of plant-herbivore interactions (shared hosts) to study inter-annual change in interaction networks and its impact on the persistence of species at different successional stages. They found that as time advances, network reorganization makes it more and more difficult for new colonizers to establish. They used a niche-overlap framework (MacArthur and Levins, 1967; Saavedra et al., 2014) to estimate herbivore competition as the number of shared plants, and a structural stability analysis (Rohr et al., 2014) to measure inter-annual changes in stability and in the parameter space that promoted feasible stable equilibriums. They found that early-arriving species increase their likelihood of persistence as time advances, while the reorganization of their interactions increasingly impedes late-arrivers to colonize.

Multilayer networks can also be used to study adaptive networks, with layers representing different temporal instances of a community. In addition to the insights provided by studies like the ones discussed, multilayer networks can provide a unified framework to test hypotheses related to the temporal structure of the community (Pilosof et al., 2017). For example, if one has a community that gains and loses species over time, the multilayer network would include all species as physical nodes, and interlayer connections would represent changes in presence/absence status. With this, one could test if the modular structure in each layer is affected by changes in species persistence by randomly reshuffling interlayer connections and comparing observed patterns to the ones obtained by random. Equal footing networks can also be used for this purpose, for example, Mougi (2016b) showed that communities with antagonistic and mutualistic interactions have an increased stability when there is interaction change across time.

As these studies exemplify, the potential of these frameworks to include multiple types of interactions and temporal or spatial scales at the same time will surely bring us a much more realistic knowledge of ecosystems. The relationship between structure and function has been studied in a mainly linear way, in which structure is assumed to be the cause of function. However, structure itself is influenced by function, and we have just seen how studies that incorporate different spatial and temporal scales are beginning to shed light on how many ecological, evolutionary and social factors can alter them. In the last section I will describe some other insights into how these factors can change ecosystems' structure and dynamics.

4. The forces that shape network structure and function

When an ecological network is defined, by choosing nodes and links, a decision is made on what elements and processes will form the system. Consequently, everything that is not included, epistemologically, becomes an external force. As we have seen, there is much to learn on how the internal properties of networks shape each other, but this knowledge will not be complete if we do not address the role of the external processes that are left aside. Here, I will show some of the main topics that are currently being studied on how ecological, evolutionary and social aspects impact the function of ecological networks. This is a very relevant line of work as ecological networks permanently interact with such forces, and in the spirit of ensuring ecological integrity, understanding their interrelation is necessary to make informed decisions on how to manage ecosystems.

4.1. Phylogenetics

Phylogenetic distances are known to influence the probability of species to interact, and rapid evolution of functional traits has been demonstrated in several contexts (Thompson 1998; Koch et al., 2014). This means that feedbacks between ecological and evolutionary dynamics can influence the structure of networks even at short time scales (Thompson 1998; Fussman *et al.* 2007; Montesinos-Navarro et al., 2019). In this context, Raimundo et al. (2018) propose the use of phylogenetically informed adaptive networks for application in restoration ecology. According to their proposal, eco-evolutionary networks using phylogenetically-structured interaction data can help predict the results of manipulation species composition in terms of robustness, resilience, or functional diversity (Devoto et al., 2012; Montoya et al., 2012; Kaiser-Bunbury et al., 2017). For example, when an invasive species is added to a network where it lacks eco-evolutionary history, a rapid adaptive evolution process can be triggered (LaRue et al., 2017), resulting in changes in the previous interaction network that may or may not be reversible by simply eliminating the invasive species. Knowing the phylogenetic background of ecologic systems can thus be relevant for management that looks to preserve its diversity, resilience or other integrity-linked concepts at the face of species invasion or loss.

4.2. Species traits

Species traits like foraging behavior, defenses against predation (López-Carretero et al., 2018), mobility (Kefi et al., 2016) or plasticity (Gray et al., 2021) can shape or restrict interactions among them. For example, defensive metabolites in some tropical species have been shown to positively correlate to the specialization and diversification of herbivores, resulting in plants that maintain a very high herbivore richness (Kursar et al., 2009; Becerra, 2015; Richards et al., 2015). Also, the simultaneous expression of foliar toughness, trichome density and phenolic content in plants can influence the strength and selectivity of herbivore-plant interactions (López-Carretero et al., 2018). Feeding mechanisms have also been found to be related to network architecture, for example, granivorous insects, leaf miners, frugivores, leaf chewers and sap suckers are much more specialized and tend to form more modular structures than xylophages and root feeders (Novotny and Basset, 2005; López-Carretero et al., 2018). When showing plastic responses, organisms can have changing effects on their surroundings, a phenomena that has been shown to alter the ecosystem services they provide (Gray et al., 2021). In this sense, knowledge about how species traits influence their role in communities can hint towards management actions that pays attention to those species which play important or endangered functions.

4.3. Habitat disturbance

Disturbance, spontaneous or recurrent, human induced or not, is known to significantly alter ecosystems (e.g. Roxburgh et al., 2004; Krebs et al., 2010). Changes in tree canopy, light availability, rainfall patterns, or soil cover are just some examples of ecosystem changes that impact species in different ways. For example, tree removal implies the disappearance of herbivores that depend on them, but it can also facilitate the production of young leaves on the remaining plants which suddenly have a better access to light, indirectly benefiting other herbivore species (López-Carretero et al., 2018). Indeed, habitat changes have been shown to have an impact on network parameters, like in the work of Valladares et al. (2006, 2012), who showed how forest loss diminished the richness, size and connectance of a plant-herbivore network as a function of the remaining fragments' size. Just as López-Carretero et al. (2014) found an increase in generalist species and connectance when resources were scarce because of normal seasonal changes, Araujo et al. (2015) found the same tendency in several empirical networks under anthropogenic land use change. If we understand how certain disturbances affect different aspects of networks, we could design better restoration plans that work in synergy with the tendencies that arise from the systems' structure.

4.4. *Agricultural management*

Agriculture is recognized as a major source of ecosystem alteration, as it covers around 40% of earth's surface (Foley et al., 2005). Nevertheless, not many examples exist that analyze agroecosystems from a network perspective (Pocock et al., 2012; Bohan et al., 2013). The insights that network theory has brought to ecology remain mostly unexploited in the agricultural context, a lag in knowledge that must be overcome. Such a system-level approach holds the potential to guide our actions around major issues like autonomous pest control, disease outbreaks and biodiversity conservation in agricultural landscapes (Vandermeer et al., 2010, 2018; Ramos et al., 2018). From an evolutionary perspective, agroecosystems are tightly integrated ensembles because they are subjected to artificial selection at both the species and the community levels, a characteristic that distinguishes them from other ecosystems. The study of agroecosystems could thus help us address how selection on multiple species assemblages shapes ecosystem structure and function (Benítez et al., 2014).

A very interesting line of research deals with the repercussions of different types of agricultural management on ecosystem structure and function. For example, Sosa-Aranda et al. (2018) showed that management intensity in coffee plantations decreased lepidopteran diversity, but increased leaf damage. This suggests that as shade trees are removed with increasing management intensity, a few specialist species are lost but many herbivores that normally feed on trees are recruited by coffee, explaining the higher leaf damage. Importantly, this implies that non-intensive management that favors shade canopy can contribute to the conservation of Lepidoptera, while also decreasing leaf damage to coffee plants. On a different approach, Vandermeer et al. (2018) modelled the dynamics of the coffee rust disease using spatially explicit networks and found that the patterns formed by plants that are below a critical distance from each other have an effect on the transmission process. Because planting density changes with management intensity, this implies that plantations along an intensity gradient will have infection rates that could presumably alter the outcome of the disease.

Because agriculture alters landscapes, the impact of different management types should also be assessed at broad spatial scales. It has been shown that patches of habitat distributed among an agricultural matrix can show source-sink dynamics (Perfecto and Vandermeer 2015). Furthermore, different types of agricultural management play a role in determining how different species perceive the landscape and whether they are able to sustain viable populations in it or not (Perfecto et al., 2009). In a metacommunity approach using multiple interaction networks, Ramos et al. (2018) showed that the combination of habitat availability, spatial distribution of habitat fragments, and permeability of agricultural patches regulates the persistence of species at a landscape level. These and other applications of network theory can help farmers and other social actors in the assessment of different management scenarios with differential repercussions on the function of ecosystems.

5. Conclusion

Given that the term ecological integrity is commonly employed in the public agenda, I have exposed its evolution and implications. However, this revision coincides with recent work which has questioned the pertinence of the concept because of its loose definitions (Rohwer and Marris 2021; Marris and Rohwer 2022). It is true that in the name of ecological integrity, many methods for assessing, monitoring and managing ecosystems have been created and that they have proven useful tools to counter the degradation of ecosystems (Karr et al., 2022). Nevertheless, employing the concept of integrity obscures the fact that a judgement of value has been made in order to determine the state variables that are deemed desirable, such as biodiversity or resilience, and it obscures for whom and by whom these cultural preferences are being defined (Marris and Rohwer 2022). Like the most recent approaches with ecological networks show, terms with formal definitions such as richness, persistence or functional diversity are a better choice for assessing the state of ecosystems, and they should be accompanied by a clear statement of why these aspects are deemed desirable.

Following this logic, I focused on the most recent methodological tools for assessing ecosystems from a complexity framework, particularly with ecological networks. I reviewed how single interaction networks have been used to study the relationships between structure and function of biotic assemblages, highlighting the contradicting results that probably stem from both methodological differences and the real word complexities that these studies have left aside. Then, I showed recent advances in multiple interaction networks and adaptive networks, that bring a more realistic view of ecosystems by allowing the integration of several types of interactions and any spatial and temporal scales in the same analysis. Together, these studies have taught us a lot about the way in which interactions among species shape their dynamics and how these dynamics can in turn change their interactions. Exciting lines of research have started to evaluate the role of cultural, evolutionary and other ecological processes in the shaping of networks. For example, studies on succession have revealed that networks rewire through time in a non-random way that has an effect on the persistence of species through its different stages (Villa-Galaviz et al. 2012; Saavedra et al., 2017). Also, phylogenetic history and body traits can inform on the probability of species to interact with each other, a fact that can be used both to infer present networks and to build possible evolutionary scenarios (Raimundo et al., 2018). Finally, some studies have assessed the effects on ecological networks of important human activities like agricultural management and land use change (de Araújo et al., 2015; Ramos et al., 2018; Sosa-Aranda et al., 2018). Together, these frameworks can be used to answer questions that can guide the management of natural resources at different spatiotemporal scales and inform on the effects of human activities on ecosystems such as production, restoration, and conservation.

This review showed that the study of the state of ecosystems is an area in continuous development. The analysis of the relationships between the structure and function of ecosystems has led to a diversity of frameworks, from integrity indexes to complex network analyses. Along the way, concepts have evolved from being morally-charged to being formally defined, and implicit subjectivities are starting to get recognized. As frameworks are increasingly able to encompass different types of processes and scales, future challenges will probably include how to balance weights and assign units to qualitatively different processes, how to couple different spatial and temporal scales, and how to deal with the increasing number of parameters that tend to come with more detailed models. Although computational capacity keeps increasing, researchers will need to be careful not to get lost in ever increasing models to the point of losing interpretability. Additionally, no model is ever complete or free from the subjectivities of those who make it, so caution should be taken to avoid confusing the use of complexity-based tools with the use of a complexity-based philosophy. The use of huge amounts of data and sophisticated models does not guarantee a complete grasp of a complex phenomena and it certainly does not free our studies from our personal biases. Indeed, simple qualitative models have brought huge insights and the most elaborate models have been used to justify prejudices. Thus, when measuring ecological integrity or when using any model to define the state of ecosystems, it is necessary to recognize the assumptions and value judgments behind our criteria, and to understand their limitations. Furthermore, rather than trying to assess phenomena with one all-inclusive model, it is a better strategy to employ several smaller models with different assumptions and different trade-offs between interpretability, precision, generality and realism (Levins 1966).

6. Glossary

Information theory: Information theory is the mathematical treatment of the concepts, parameters and rules governing the transmission of messages through communication systems. Abstractly, information can be thought of as the resolution of uncertainty.

Network theory: The study of graphs as representation of relationships between discrete objects with the use of nodes and edges with certain attributes.

Types of ecological networks

Adaptive networks: Networks whose structure is allowed to change through time.

Equal footing networks: Multiple interaction networks where all types of interaction are summarized by the sign of the effect they produce in the interacting species. Hence, the community matrix can include (0,0), (0,+), (0,-), (+,0), (-,0), (+,+), (-,-), or (0,0).

Extended food webs: Multiple interaction networks where trophic interactions are modelled through differential equations, which then incorporate non-trophic interactions as functional modifiers or their parameters.

Multilayer networks: Networks where a set of physical nodes exist in several layers, with each layer representing a particular aspect of layering (for example, interaction type), and both intralayer and interlayer nodes.

Multiple interaction networks: Networks that encompass different types of ecological interactions, for example, predation, mutualism, commensalism, amensalism, etc.

Single interaction networks: Networks that are defined by only one type of ecological interaction, for example, food webs or pollination networks.

Concepts linked to ecosystem function (adapted from Saint-Béat et al. (2015); Ramirez-carrillo et al. (2018); Walker et al. (2016); Landi et al. (2018)):

Adaptability: self-organization in the face of external changes without system-level intent or centralized control.

Adaptive cycles: characteristic phases for the dynamics of ecosystems characterized by Holling (1986, 2001). Composed of phases of growth and flexibility, stabilization and loss of flexibility, structure collapse and reorganization.

Extinction cascade: measures the loss of additional species after the removal of one target species. Species removal can be random or targeted.

Invasibility: the propensity of a system to be invaded by new species.

Persistence: the time for a variable to remain in the same state before changing to a different one (Pimm and Pimm, 1991; Loreau et al., 2002).

Resilience: the capacity of a system to experience perturbations and return to the same structure and functions. It follows Holling's (1973) notion of the amount of disturbance a system can take without shifting to an alternate regime, assuming there are various stable states. Engineering resilience is the rate at which a system returns after a disturbance to the equilibrium state, assuming that there is only one stable state (Holling 1996; Gunderson 2000).

Robustness: relates to the durability of the stability of the system. It is a measure of the amount of disturbance an ecosystem can endure before it changes to a different state. (Loreau et al., 2002). In network analysis, it is often measured as the ability of the system to resist extinction cascades (Borrvall et al., 2000; Dunne et al., 2002a).

Stability (linear): used in theoretical studies, where each entry of the community or Jacobian matrix usually quantifies the change in population growth rate of species *i* caused by a small perturbation in the abundance of species j around an equilibrium (Novak et al., 2016). Linear stability is defined by the real part of the leading eigenvalue of the Jacobian matrix. If it is positive, the equilibrium is unstable. Otherwise, it is stable. Moreover, if stable, the inverse of the absolute value of the real part of the leading eigenvalue gives an indication of the time needed by the system to return to its equilibrium, a measure of resilience. Global (vs. local) stability implies that any (vs. small) perturbation from the equilibrium will be dampened.

Stability (structural): it refers to the probability of coexistence of all the species in the ecosystem. An equilibrium at which all the species coexist with positive abundances is called feasible. The region in parameter space for which the system has a feasible equilibrium is its domain of stable coexistence, and its size gives a probability of its structural stability. The bigger the domain, the more structurally stable the system is (Rohr et al., 2014).

Sustainability: the most frequently-quoted definition is "development that meets the needs of the present without compromising the ability of future generations to meet their own needs".

Measures of network structure (adapted from Landi et al. 2018):

Connectance: total number of realized interactions divided by the number of possible interactions.

Connectivity: total number of interactions

Linkage density: average number of interactions per species

Modularity: depicts the extent to which a network is compartmentalized into groups where species are strongly interacting with species within the same module and less so with species from other groups (Olesen et al., 2007).

Nestedness: It is a pattern of interactions in which specialists can only interact with a subset of species with which more generalists interact (Bascompte et al., 2003).

Node degree distribution: the distribution of the number of interactions per species. A generalization of the node degree distribution is the interaction-strength distribution, taking into account the weights associated with each link (Newman 2010).

Species dependence: the dependence of a species *i* on a species *j* is defined as the fraction of interactions between *i* and *j* relative to the total number of interactions of species *i* (Bascompte et al., 2006; Vieira and Almeida-Neto 2015). In this context, a **species strength** refers to the sum of dependences of the mutualistic partners relying on it.

Species richness: number of species

Trophic species: a functional group of species sharing the same set of predators and prey. While it avoids redundancy of interactions, it is now recognized that redundancy can be important for ecosystems.

Weighted connectance: the weighted linkage density divided by species richness.

Weighted linkage density: considers the proportion of biomass flow to weight the contribution of each link to and from all equivalent species. Equivalent species are defined using the Shannon metric of entropy (Shannon 1948).

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Data availability

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CAPÍTULO II

EFECTO DE LAS INTERACCIONES DE ALTO ORDEN EN LA ROBUSTEZ DE LA ESTRUCTURA DE LA RED DEL CAFETAL

PREFACIO

Existen muchas formas de representar las comunidades biológicas y de medir su funcionamiento. Una rama de la investigación que ha sido particularmente útil para estos propósitos es el estudio de los sistemas mediante el uso de redes, donde los nodos representan especies o conjuntos de especies y las aristas representan las interacciones que mantienen entre sí (Landi et al., 2018). Esta forma de representación es por un lado intuitiva y por otro, muy poderosa. Una vez definidas, las redes ecológicas nos permiten medir, por un lado, la estructura con que está construída la comunidad, y por otro, las características funcionales que esta estructura confiere al sistema.

Existen una serie de métricas y conceptos ligados a la estructura de las redes que nos hablan de su funcionamiento, y una de las más usadas es la de la robustez. La robustez se puede definir de muchas maneras, pero una de las más intuitivas y utilizadas se refiere a la velocidad con que la estructura de la red se va desconectando conforme pierde sus componentes, sean nodos o aristas (Bascompte & Stouffer 2009; Bellingeri & Cassi 2018). En este caso, debido a que los nodos representan grupos biológicos y las aristas representan interacciones ecológicas entre los grupos y que son necesarias para su supervivencia, un nodo que queda desconectado puede pensarse como una especie que se extingue. Así, mucho se ha aprendido representando las comunidades como redes y "atacándolas" mediante la remoción de nodos o aristas para después medir qué tan rápido se desconectan: mientras más lento se desconecten, más robustas asumimos que son. Sin embargo, hasta donde llega nuestro conocimiento, este tipo de análisis nunca se ha utilizado para estudiar una red que incluye interacciones de alto orden.

Por lo tanto, en este capítulo nos ocupamos en primer lugar de definir la red asociada al cafetal que es nuestro sitio de estudio mediante la revisión bibliográfica de la literatura preexistente sobre las interacciones ecológicas que se conocen en el lugar. Mediante la sistematización de dicha información pudimos definir una red ecológica con 22 nodos. Debido a que las redes en su definición clásica matemática no pueden incluir interacciones de alto orden, tuvimos que proponer un método nuevo en el que éstas son transformadas en pseudo-nodos para así trabajar con una red clásica a la que puede aplicarse todo el aparato metodológico que se ha venido desarrollando en el campo de las redes matemáticas desde hace décadas. Una vez obtenida la red, hicimos un análisis de robustez ante la pérdida de nodos en orden aleatorio y por orden descendiente de grado, comparándola en la red con y sin interacciones de alto orden (pseudonodos). La robustez la medimos de dos formas, primero, con un índice conocido en la literatura que adaptamos para funcionar con interacciones de alto orden en forma de pseudonodos. Después, la medimos mediante la forma de la cascada de extinciones secundarias provocadas por la misma remoción de nodos. Además, utilizamos análisis de centralidad de nodos y modelos nulos en los experimentos de robustez para descartar efectos de la introducción de pseudonodos sobre los resultados.

En general, encontramos que la robustez de la red con interacciones de alto orden es mayor o igual que su contraparte sin interacciones de alto orden, dependiendo del orden de remoción de los nodos. También encontramos que el método que propusimos para representar las interacciones de alto orden como pseudonodos es útil y no genera artefactos en los resultados, como se comprobó con el uso de modelos nulos y estudios de centralidad de los nodos.

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High-order interactions maintain or enhance structural robustness of a coffee agroecosystem network

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ABSTRACT

The capacity of highly diverse systems to prevail has proven difficult to explain. In addition to methodological issues, the inherent complexity of ecosystems and issues like multicausality, non-linearity and context-specificity make it hard to establish general and unidirectional explanations. Nevertheless, in recent years, high order interactions have been increasingly discussed as a mechanism that benefits the functioning of highly diverse ecosystems and may add to the mechanisms that explain their persistence. Until now, this idea has been explored by means of hypothetical simulated networks. Here, we test this idea using an updated and empirically documented network for a coffee agroecosystem. We identify potentially key nodes and measure network robustness in the face of node removal with and without incorporation of high order interactions. We find that the system's robustness is either increased or unaffected by the addition of high order interactions, in contrast with randomized counterparts with similar structural characteristics. We also propose a method for representing networks with high order interactions as ordinary graphs and a method for measuring their robustness.

1. Introduction

The link between an ecosystem's diversity, structure and functioning has long been debated in ecology. Both empirical and theoretical studies have tried to decipher the nature of their relationship and the factors that take part in shaping it. On the one hand, the existence of different definitions for these features has contributed to the difficulty of the task, while on the other hand, an intrinsic complexity stems from the very numerous elements, processes and scales that interact to give rise to these qualities (Ives and Carpenter 2007). Early ideas on the topic focused on the notion of stability, and maintained that diversity made ecosystems stable through species limiting each other's growth by predation or competition (Odum 1953; MacArthur 1955; Elton 1958). These notions were dramatically challenged by the work of Robert May (1972; 1973), who used linear stability analyses to show that communities modelled as random networks lose local stability as the number of species, the number of interactions, or their strength rise. These results caused commotion in the scientific community, as they seemed to contradict the very real biodiversity found around the world. Since then, two main extensions have helped reconcile theory with observation; mainly: the use of realistic community structures (Lawlor 1978; Lawlor 1980) and the complementation of linear stability analyses with other methods to assess ecosystem function from both a structural and a dynamical point of view like robustness, feasibility or structural stability (Landi et al., 2018). It is now generally recognized that diversity tends to positively correlate with some measures of ecosystem functioning, like stability, robustness or productivity. Nevertheless, this does not mean that diversity is the direct driver of these traits, rather, it should be regarded as an 'umbrella' indicator of many ecological mechanisms that are inherent to ecosystems and that are the actual determinants of the diversity-function relationships (McCann 2000). Such mechanisms and how they may favor the assembly and reproduction of highly diverse communities are now the focus of many studies (Chesson 2000; Levine et al., 2017).

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Different mechanisms have since been proposed to enable the coexistence of species in highly diverse systems (Chesson 2000; Wright 2002; Adler et al., 2013; Levine et al., 2017). Recently, high order interactions (HOI) have been proposed as a key mechanism for the persistence of diverse communities (Bairey et al., 2016; Grilli et al., 2017). HOIs have been defined in subtly different ways and they have sometimes been equated with the concept of indirect effects (Worthen and Moore 1991; Billick and Case 1994; Sanchez 2019). Nevertheless, we align with those authors who have pointed out the strong differences between these two and define them as follows (Billick and Case 1994). Indirect effects are changes in interactions that are solely mediated by population densities (Levine 1976), and therefore pass from one species to another via the density changes in one or more intermediary species. These can also be called "interaction chains" (Wootton 1993). On the other hand, HOIs are functional modifications in the interaction of two species caused by a third one, and need not pass through any change in population densities (Wootton 1993). Indirect effects are a logical consequence of pairwise interactions whenever there are more than two species involved, while HOIs occur through additional mechanisms that cannot be extrapolated from isolated pairwise interactions. The importance of HOIs has been widely recognized, as they are quite common and can have substantial implications: ecosystem engineering, predatory adaptive behavior, changes in foraging, facilitation, mutualisms and many so-called trait-mediated effects commonly involve HOIs (Beckerman et al., 1997; Werner and Peacor 2003; Holt and Barfield 2012; Kéfi et al., 2012; Bairey et al., 2016). Bairey et al. (2016) computationally explored the role of HOIs on the linear stability and feasibility of systems described as virtual random networks and found that HOIs could indeed attenuate or even revert a negative relationship between the number of species and stability.

While the findings of Bairey et al. (2016) and other recent theoretical work have greatly contributed to our understanding of the relationship between HOIs and species coexistence (Grilli et al., 2017; Singh and Baruah, 2020; Li et al., 2020), they rely on hypothetical networks whose interactions are set randomly and do not represent known ecological interactions, or on the assessment of some focal species (Mayfield and Stouffer, 2017). It thus remains unclear how HOIs may affect the function of empirically-documented networks which, arguably, capture some aspects of their structure and dynamics in a more faithful manner. There are now some well-studied ecological and few agroecological networks that could help fill this important gap (Scheffer 1997; Yoon et al., 2004; Fortuna et al., 2014; Perfecto and Vandermeer, 2015; López Martínez 2017). Agroecosystems cover around 40% of the Earth's surface (Foley et al., 2005), represent a substantial part of the world's biodiversity, and have just recently begun to be analyzed from a network perspective (Bohan et al., 2013; López Martínez 2017). The insights gained from such a system-level approach hold the potential to guide our actions around major issues like autonomous pest control, disease outbreaks and biodiversity conservation in agricultural landscapes (Vandermeer et al., 2010, 2018; Ramos et al., 2018).

With this in mind, in the present study we updated and analyzed an empirically-based network for a coffee agroecosystem in southern Mexico. This biodiverse agroecosystem has been studied for about three decades and many of its species and interactions have been thoroughly described (Perfecto and Vandermeer 2015). Importantly, different HOIs have been found to play a key role in the dynamics of the main coffee pests and their natural enemies (Vandermeer et al., 2010; Perfecto et al., 2021), motivating discussions on different formalisms to integrate HOIs to ecological network analyses, which remain an underdeveloped area (Golubski et al., 2016; Battiston et al., 2020). Thus, we analyzed the coffee agroecosystem network from a structural perspective in order to investigate the effects of HOIs on the overall robustness of this system, defined as its capacity to remain connected in the face of node removal representing species loss. To this aim, we propose a method for representing networks with high order interactions as ordinary graphs and a method for measuring their robustness which is a modification of Piraveenan et al. (2013). Our work aims to contribute to the understanding of the mechanisms underlying species coexistence in highly diverse systems, as well as to provide novel insights that can inform management practices based on the biological understanding of agroecosystems.

2. Methods

2.1. Study site

The study site is "Finca Irlanda", a 320 ha coffee plantation situated on the highlands of El Soconusco, Chiapas (158,110 N, 928,200 W; 900 masl). Precipitation in the region averages 4500 mm per year and the vegetation type is seasonal tropical forest. Nevertheless, primary vegetation has been almost completely replaced by coffee plantations with different management intensities, aside from some tiny fragments of original forest kept in some farms. In Finca Irlanda, there is a portion of such original vegetation set aside for conservation, while the management of the surrounding productive area involves keeping the shade provided by native trees, which, among other practices, make it a highly biodiverse agroecosystem (Perfecto and Vandermeer, 2015).

It is convenient to detail some parts of the complex ecological web found in the study site. There are four main antagonists of coffee plants: the coffee leaf rust, *Hemileia vastatrix*, the coffee berry borer, *Hypothenemus hampei* (see Fig. 3d further), the coffee leaf miner, *Leucoptera coffeella*, and the coffee green scale, *Coccus viridis* (Fig. 3c). The last one keeps a spatially clustered mutualistic relationship with ants of the *Azteca* genus (Fig. 3e), which feed on the honeydew produced by the scales while protecting them from being eaten by a lady beetle, *Azya orbigera*. Thanks to this protection, the scale populations reach high levels within the clusters, which in turn increases their probability of being infected by the white halo fungus, *Lecanicillium lecanii*, a fungus that is also capable of infesting the coffee rust. By patrolling coffee plants where green scales feed, *Azteca* keeps other herbivores, like the berry borer beetle or the leaf miner from establishing big populations on these plants. However, all the effects that the *Azteca* ants have on the system are temporally inhibited by flies in the genus *Pseudacteon* (Family: Phoridae), who are parasitoids of the *Azteca* ants, and that cause them to retreat to their nests, hide or dramatically reduce their movement whenever they sense a fly nearby. This inhibition of *Azteca* leaves the scales and the coffee plants unprotected for a period of time, a lapse that has been proven to be ecologically relevant and that for example, is enough for allowing *Azya orbigera* to prey on the scales or oviposit underneath them, ensuring nourishment for their future larvae (Liere and Larsen 2010; Vandermeer et al., 2010).

The system here described exhibits different kinds of direct interactions like herbivory and parasitism, but also numerous HOIs (Table S1). For example, *Azteca* ants exert a second order interaction when they inhibit the predation interaction among *C. viridis* and *A. orbygera* by harrasing the latter, mostly without harming it (Vandermeer and Perfecto 2006; Liere and Larsen 2010; Vandermeer et al., 2010). An example of a third order interaction is the effect of the phorid flies, which by paralyzing or chasing away *Azteca* ants, inhibit the second order interaction they exerted and thus enable the predation of *C. viridis* by *A. orbygera* (Hsieh et al., 2012).

2.2. Network inference

We used a network approach to analyze the community under study. Species were represented as nodes whose connections were defined by the ecological interactions among them. In order to define the network's structure, we reviewed published information on this particular agroecosystem and integrated it in a common database.

The reviewing process began with a book that collects over 20 years of research in the area (Perfecto and Vandermeer 2015). All referenced papers that explained, observationally or experimentally, at least one ecological interaction among a pair of species, were examined too. The type of interactions and the direction of their effects were extracted, including qualitative information about their strength, whenever available. If any of the papers in this first group made reference to other investigations in the area, those were also revised. All the information was integrated in a database organized as follows: *transmitter node (*e.g. *H. hampei), recipient node* (e.g. *Coffea), kind of interaction* (e.g. +/-), *description* (e.g. females of *H. hampei* bore into the coffee berries to oviposit and their larvae feed from it) and *reference* (listing of the articles that support the interaction). For HOIs, instead of a *recipient node*, a column was added with the *recipient interaction* (e.g. the presence of *Azteca* prevents *H. hampei* from boring into the coffee, inhibiting herbivory). Interactions that were uncertain, but suspected, were annotated but not considered for the construction of the network. Finally, the network was compared with smaller versions published previously and revised by experts.

We assumed that organisms in the empirically-grounded network co-occur, an assumption we regarded necessary in order to set up a model system in which we can interpret and keep track of the effects of HOI addition, without temporal changes as a confounding variable. This assumption is plausible because most of the field work underlying the network inference has been done in the same coffee plantation, a perennial system ("Finca Irlanda", in Southern Mexico), during summer, from May to August. Although seasonality in the study site is relatively mild, some fluctuations have been observed between the rainy (May to November) and dry seasons (December to April). However, interaction data underlying this network has been obtained during the rainy season, where organisms in the network exhibit altogether the largest population sizes.

2.3. Structure definition and general metrics

The structure of the network was visualized with the software *Gephi 0.9.2*. Because network-related methods only contemplate ensembles of nodes connected directly through edges (that is, first order interactions), it is not possible to define a network with edges connecting to other edges, which is the case of HOIs. For this reason, two versions of the network were created: the first one only captured the nodes and their first order interactions; the second one included HOI modified interactions as artificial pseudo-nodes, an artifact that allowed us to use the full force of network theory to analyze the system. Topological analyses were conducted on both versions of the network in order to quantify the effect of HOIs.

The transformation process of HOIs into pseudo-nodes is depicted in Fig. 1. Basically, an edge that was affected by a third node was labeled with a new pseudo-node (e. g. a pseudo-node named "predation"), so the third node now had a simple edge connecting it to the new pseudo-node. The same logic works for second, third or any higher order interactions. A similar procedure was suggested by Newman (2018), where interactions involving more than two nodes are introduced by adding new nodes belonging to a different category as part of a bipartite graph. This new node is connected by a single edge to each original node. However, this procedure is limited as bipartite graphs do not account for edges between nodes belonging to the same category.

Once both versions on the network were obtained, standard network metrics were quantified in order to characterize them and as a way of exploring how much pseudo-node addition changed the general structure of the network. In particular, we analyzed node relevance according to their centrality in both webs. For this, we used two commonly used metrics that can also be interpreted in ecological terms: i) *Degree*, which points to nodes directly linked to many nodes in the network and is the simplest and most widely used measure of node connectivity (Sharma and Surolia, 2013), and ii) *Betweenness centrality*, which helps identify nodes acting as "bridges" between nodes or groups of nodes in a network; it is used to find nodes that indirectly link many nodes of the network, and the removal of which may affect the communication between many pairs of nodes or groups of densely connected nodes (communities or modules) through the shortest paths between them. Thus, nodes with high betweenness centrality may largely influence the flow of matter and energy in ecological systems (Lu and Zhang, 2013; Raghavan Unnithan et al., 2014). Even though the structure-function relationship in ecological networks constitutes an old and still open field of research, some studies have at least partially validated the use of these metrics with functional data, expert knowledge or dynamical simulations (e.g. Endredi et al., 2018; Cagua et al., 2019; Yang et al., 2021; Arroyo-Lambaer et al., 2021; Gouveia et al., 2021; Zamkovaya

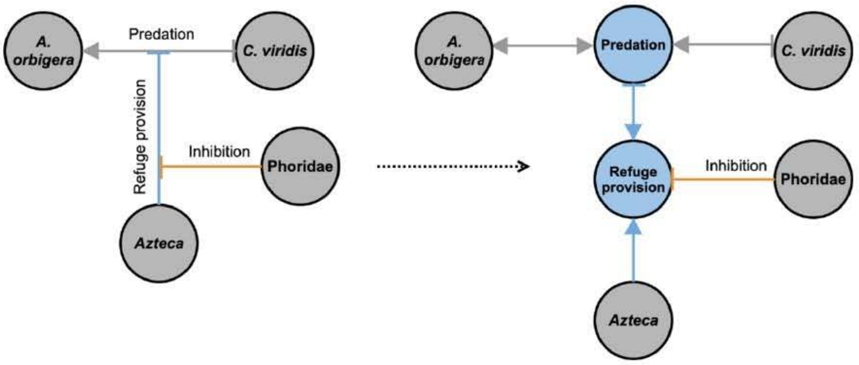

Fig. 1. Transformation process of second and third order interactions into pseudo-nodes. The grey nodes represent biological taxa and the blue nodes are pseudo-nodes representing ecological interactions which are modified by a HOI. First order edges are dark grey, second order edges are blue and third order edges are orange. Arrows represent positive effects, and crossed endpoints stand for negative effects. For example, the predatory interaction between *A. orbigera* and *C. viridis* is turned into a pseudo-node named *predation* in order to be modified by the refuge provision performed by *Azteca*, a second order interaction. The pseudo-node has two incoming positive arrows from the nodes that perform it because it needs both nodes to exist (*predation* could not occur without both prey and predator present). Likewise, refuge provision is inhibited by the presence of phorids, so it is turned into a second pseudo-node in order to be modified by the third order interaction performed by *Phoridae*. In the same way, this *refuge-provision* pseudo-node has incoming positive arrows both from *Azteca* and *predation*, because it would lose its meaning if any of them ceased to be present. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2021). All calculations were made with the software *Gephi 0.9.2*.

2.4. *The effect of high order interactions on network robustness*

We conducted a robustness analysis for both versions of the network (with and without HOIs). Robustness was measured by calculating the area under the curve that depicts the size of the biggest connected component as nodes are removed one by one from the network (Kasthurirathna et al., 2013; Piraveenan et al., 2013; Navarro Díaz 2015). This measure is compared with the area under the curve traced by a complete graph, that is, a graph where every possible pair of nodes is connected by an edge. Thus, following Eq. (1), the relationship between these two areas gives us a measure of robustness (for a full derivation of the equation see Piraveenan et al. (2013)).

$$R_1 = \frac{A_g}{A_c}\,(\%) = \frac{200\sum_{k=0}^{N} S_k - 100S_0}{N^2} \tag{1}$$

Where A_g is the area under the curve of the evaluated graph and A_c that of the fully connected graph. S_k is the size of the largest component after k nodes have been removed, S_0 denotes the initial largest component size, and N is the network size. According to the above equation, for a fully connected network of any size, the robustness coefficient (R) is always of 100% (taken from Kasthurirathna et al., 2013).

For the network that includes HOIs, only real nodes could be selected for removal, in order to avoid the biologically meaningless action of removing pseudo-nodes. Following this logic, whenever a node got selected for removal, any pseudo-node connected to it was also eliminated, since pseudo-nodes lose their meaning once the species causing the higher order effect is eliminated. Because this modification often resulted in the elimination of several nodes at the time, we modified Eq. (1) in order to control for it. In the Piraveenan et al. (2013) derivation, the area under the curve of the fully connected graph assumes one node removal per step in the x axis. If we assume n node removal per step (in order to control for pseudo-node removal in the evaluated graph), this area is $Ac = N2/2n$ and the robustness equation becomes:

$$R_n = \frac{A_g}{A_c}\,(\%) = \frac{200n\sum_{k=0}^{N'} S_k - 100nS_0}{N^2} \tag{2}$$

Where n is the average number of nodes removed at each step (1.54 in this network) and N' is the number of real nodes in the network (N minus the number of pseudo-nodes) . Eq. (1) is equivalent to Eq. (2) when $n = 1$ and there are no pseudo-nodes.

Hence, we used Eq. (1) for the network without HOIs and Eq. (2) for the network with HOIs. For each of these networks, two node removal methods were tested. With the first one, nodes were randomly selected and removed one by one until removing them all. This was done 200 independent times and a robustness average was obtained. The second method consisted of removing nodes by degree, from highest to lowest.

In order to discard the possibility that the differences between the networks with and without HOIs could be an artifact of the simple increase in node and edge number after HOI adition, we compared our results with three null models that had the same general metrics as these two webs but lacked the particular structural properties of the empirical pseudo-nodes. Following this setup, if HOIs actually confer a difference in robustness, that is, if their effect is not just due to the increase in node and edge number, we expected an increase in robustness as a result of HOI addition in the empirical web, but not in their null models. In order to test this, the robustness of each network with each removal method was also compared with the average robustness of 200 randomized but comparable networks, i.e. with the same number of nodes, average degree or interaction density. Three types of random networks were used: totally random networks (Erdős and Rényi 1960), small-world networks (Watts and Strogatz 1998) and scale-free networks (Barabási and Albert 1999). The first model generates random networks from a set of nodes in which the edges are independently created between any pair of nodes with a probability p. Because the structure of ecological networks is far from being random, we also used small-world and scale-free networks, which have been proved to share structural characteristics with many real world networks (Montoya and Solé 2002; Barabási and Bonabeau 2003). Small-world networks follow an algorithm that starts with a regular lattice where each node is connected to its k closest neighbors, and where each edge is then re-connected to a randomly chosen node with a certain probability, avoiding duplicates and self-loops. This construction produces networks with a high clustering coefficient and short paths, two particularities that have been found in many ecological webs (Montoya and Solé 2002). The last method builds networks with a preferential attachment mechanism, where nodes are added sequentially such that each new node is connected to a number m of existing nodes, where the probability to choose a node for connection is proportional to the number of links that this node already has. This creates networks with power-law degree distributions, another characteristic that has been widely found in ecological webs (Barabási and Bonabeau 2003). For the Erdös Rényi method we used the values $N = 34$ and $p = 0.095$, and $N = 22$ and $p = 0.145$ for networks representing cases with and without HOIs, respectively (where N is the number of nodes of the empirical web and p is taken from their density). For the Watts-Strogatz method, we chose $N = 34$, $k = 3$ and $p = 0.5$, and $N = 22$, $k = 3$ and $p = 0.5$ for networks representing cases with and without HOIs, respectively (where k is the average degree of the empirical web and p was arbitrarily chosen). For the Barabasi-Albert method we chose $N = 34$ and $m = 1$, and $N = 22$ and $m = 2$ for networks representing cases with and without HOIs, respectively (where m is chosen so that the resulting average degree matches the empirical average degree).

Because nodes in the empirical network with HOIs were removed along with their associated pseudo-nodes as discussed above, the randomized versions of this network needed to emulate this process too. This was done in the following way: First, we quantified the probability to remove a number n of pseudo-nodes with each real node removal in 100 simulations of the empirical network with HOIs. Then, in the randomized networks (composed of 34 nodes), a subset of 22 randomly chosen nodes was defined to stand for the real nodes, while the remaining 12 nodes stood for the pseudo-nodes. This random choice of pseudo-nodes in each simulation controls for any bias that could emerge from choosing pseudo-nodes with different centrality properties (i.e. the contrasting effects of choosing hubs and non-hubs to stand for pseudo-nodes). At each removal step, a node was removed (randomly or by degree as explained above) from the real nodes pool alongside with n nodes from the pseudo-node pool, with n drawn from the probability distribution derived from the mentioned simulations. Again, we used Eq. (1) for calculating robustness of the randomized versions of the network without HOIs and Eq. (2) for the randomized versions of the network with HOIs. With these numerical experiments we were able to compare, on the one hand, the robustness of the two versions of our network, that is, with and without HOIs, and on the other hand, each empirical robustness with their randomized analogues. One-way ANOVA tests were performed to test the significance of the differences in robustness among the networks with and without HOIs, as well as between their corresponding null models, with one ANOVA run for each of the four network structures (one empirical and three randomized null models) in each of the two node removal methods (i.e. eight total pairwise comparisons).

Using the same experimental design, we quantified secondary extinctions in order to complement the measure of robustness with a more direct and easily interpreted measure. For this, we counted the number of nodes that became isolated along with each node removal. Because isolated nodes by definition have no interactions with any other nodes in the system, we considered them to become extinct. Thus, taking the primary extinctions (sequential node removal) and the secondary extinctions (isolated nodes) into account, we quantified the proportion of remaining nodes in the community at each removal step. This approach has been used by previous authors to assess and compare robustness across ecological systems (Cai and Liu 2016). Simulations were done with the library NetworkX 2.5 (Hagberg et al., 2008) in *Python 3.7.1.* and ANOVA tests were performed in *RStudio 1.2.1335* (RStudio Team 2020). Scripts are publicly available at: https://github.com/laparcela/CoffeeNetworkStructure

3. Results

3.1. Network inference

From literature revision, 48 interactions between 22 nodes were established out of 44 scientific papers and books, all conducted in our study site (Fig. 2). This information is organized in the supplementary material table S1.

3.2. Structure definition and general metrics

Two versions of the web were obtained with *Gephi*, the first one containing only first order interactions and the second one after adding pseudo-nodes for HOIs (Fig. 3).

Without HOIs, the network is composed of 22 nodes and 68 interactions, while incorporating HOIs makes it a network of 34 nodes and 104 interactions. Both networks have an approximate average degree of 3. Centrality analysis showed that *C. viridis, Coffea, H. hampei, Azteca, Pheidole* ctp. and *Pseudomyrmex* spp are the nodes with the highest rankings in both networks and for different centrality metrics (Fig. 4). Thus, even though HOI addition results in a larger web, relevant properties like connectivity and single-node centralities remain largely unaltered. Additional metrics for both versions of the network are available in Table S2.

3.3. The effect of high order interactions on network robustness

Fig. 5 presents the results of the robustness analyses for the empirical coffee networks with and without HOIs, as well as the results for the three different types of randomized networks with comparable structures. In the case of the empirical networks, the addition of HOIs did not significantly change the network robustness under random node removal, but robustness increased significantly under directed node removal. In contrast, for the three types of randomized networks that we used as null models, those with the same node number, edge degree and density as the empirical network with HOIs significantly lost robustness under the two node removal protocols, except for the completely random networks (Erdos-Renyi) under random removal, which showed no significant changes. Additionally, in the node removal by degree, taking HOIs into account made the empirical network more robust than all its randomized counterparts. Statistically significant differences are

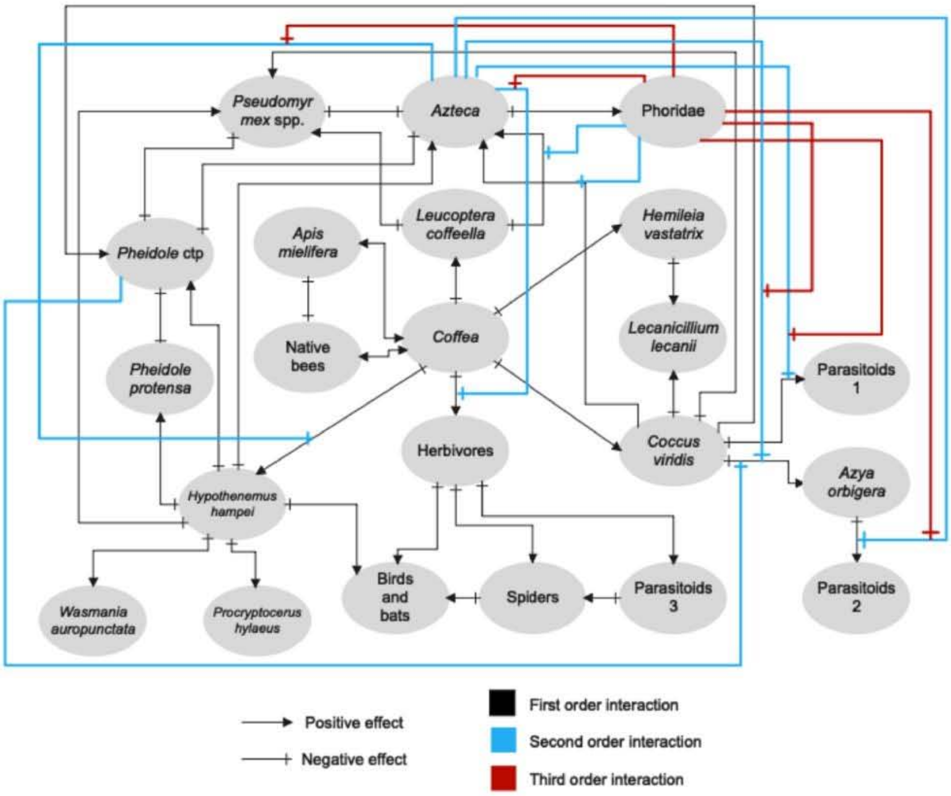

Fig. 2. Complete network before transformation from HOIs to pseudo-nodes. Black lines are first order interactions, blue lines are second order interactions and red lines are third order interactions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

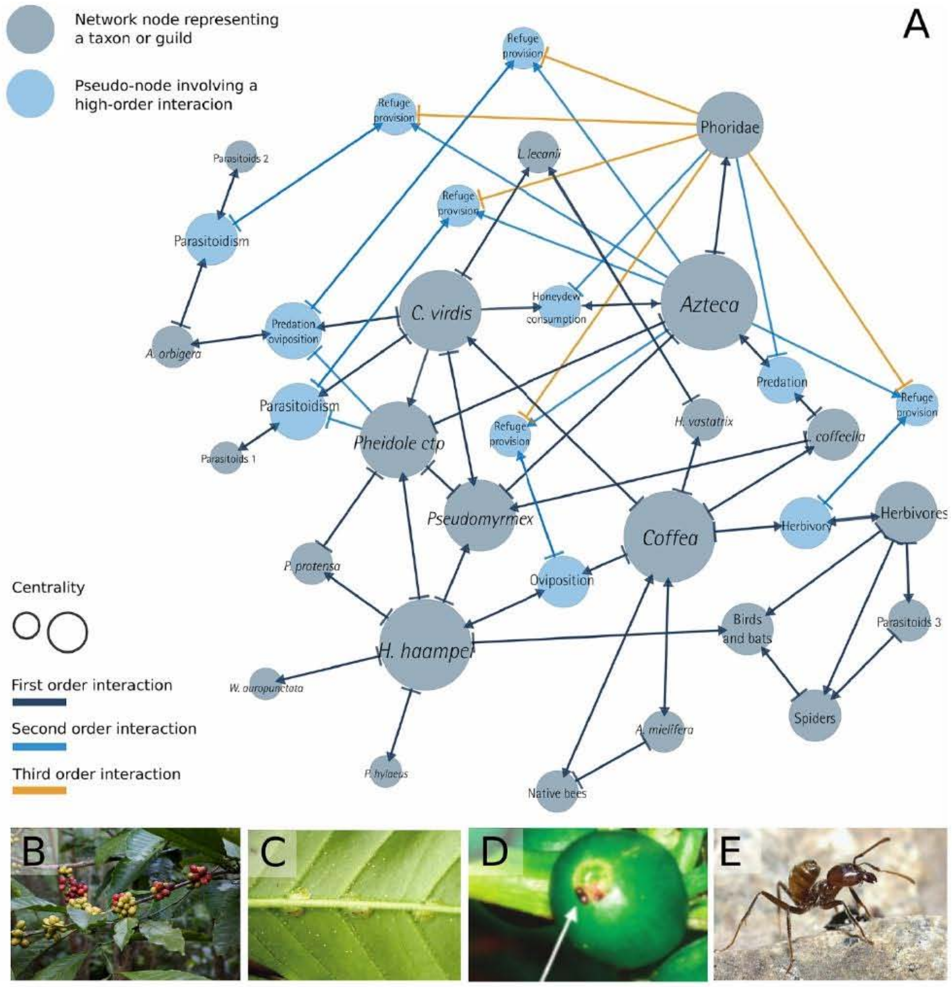

Fig. 3. A: Community network with first, second and third order interactions. Grey nodes represent biological taxa and blue nodes are pseudo-nodes representing ecological interactions which are subject to being modified by a HOI. Node size is determined by its degree. First order edges are grey, second order edges are blue and third order edges are orange. B: Coffee plants (*Coffea*). C: Coffee green scale (*Coccus viridis*), a potential pest in the system. D: Coffee berry borer (*Hypothenemus hampei*), one of the main coffee pests, about to penetrate a coffee grain. E: *Azteca* ant, an important regulator of this interaction network. Photographs: Wikimedia Commons by *Jmhullnot* at https://commons.wikimedia.org/wiki/File:CoffeeBerry.jpg (B), John Vandermeer (C, D), Alex Wild (E). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

supported by *p* values <0.05 and large effect sizes as measured by *eta* squared, *epsilon* squared and *omega* squared indexes (Lakens 2013). The details of these statistical analyses can be found in the table S3 of the Supplementary material. Because all randomized analogues of the network with HOIs have the tendency to lose robustness, while the robustness of the actual empirical networks is either unchanged or increased by HOIs, we can say that the effects observed in the empirical networks are indeed a result of the particular structural properties conferred by HOI addition and not of simply increasing the number of interactions. Indeed, it seems that high order interactions favor robust network structures that may enable the coexistence of diverse systems.

In parallel, our quantification of secondary extinctions showed the same tendency (Fig. 6). The proportion of remaining nodes after sequential node removal and secondary extinctions shows that HOI addition results in a less abrupt diversity decline in the empirical networks, while the null models showed no differences (overlapped red and blue lines) or even a more abrupt diversity decline (more pronounced decline showed by the red lines). We believe this strengthens the results obtained by the robustness measure, and allows us to say with a clearer picture that HOIs increase the robustness of the system.

4. Discussion

We have integrated a vast set of empirical evidence into a coffee-

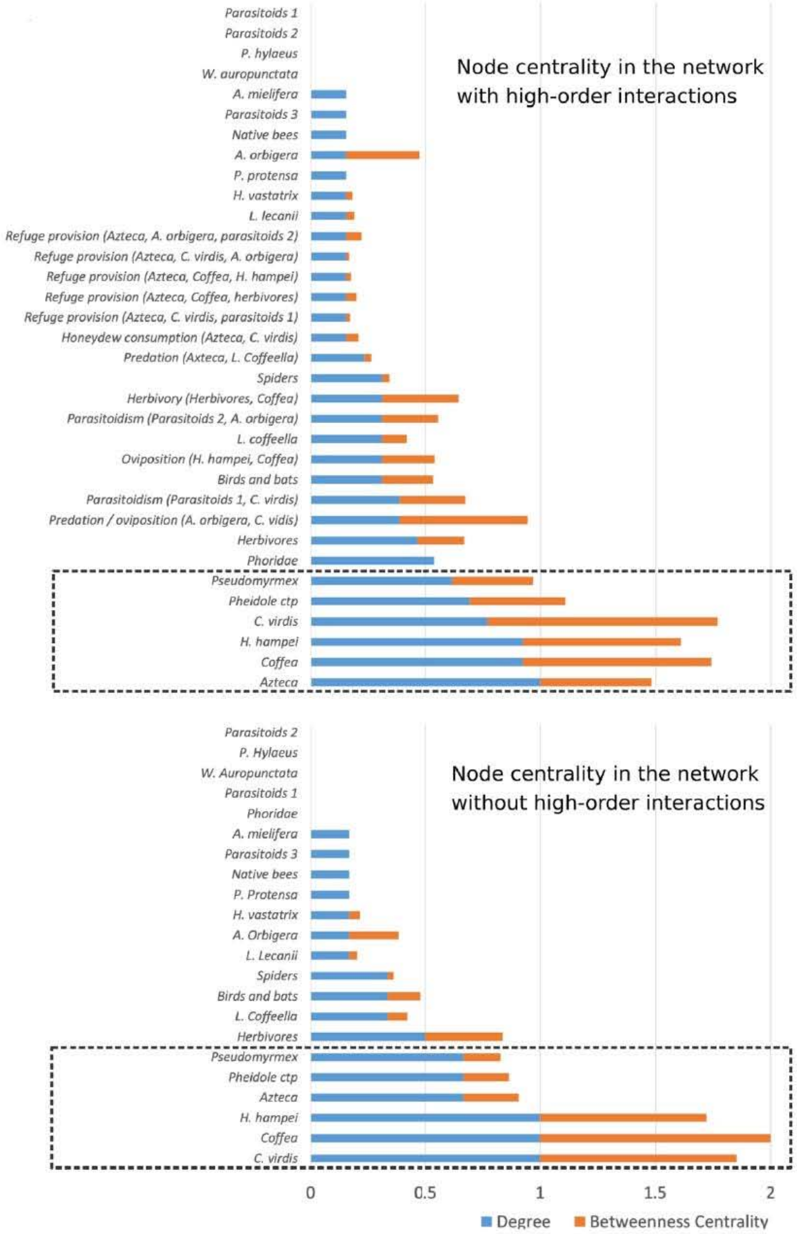

Fig. 4. Node centrality analysis for the network without HOIs (above) and with HOIs (below). *C. viridis, Coffea, H. hampei, Azteca, Pheidole* ctp and *Pseudomyrmex* spp are the highest ranking nodes in both networks.

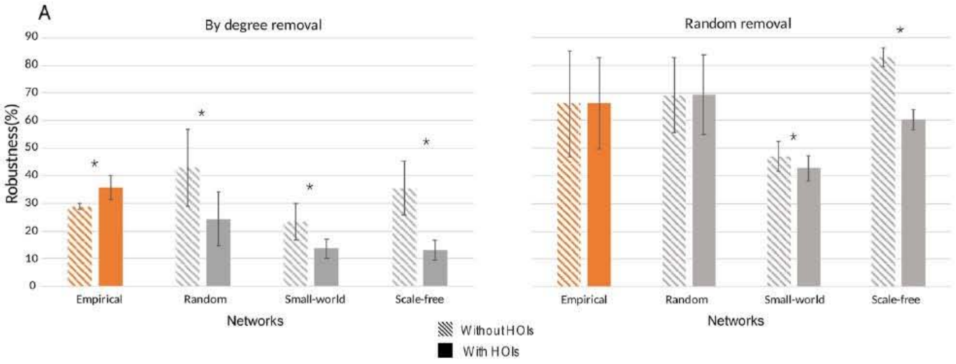

Fig. 5. Robustness of the coffee-associated network, with and without HOIs, as well as random, small-world and scale free networks with same *n*, mean degree and density. A: When removing nodes by degree, the empirical network (orange bars) is significantly more robust when HOIs are added, while the three types of randomized networks (grey bars) lose robustness when their structures are comparable to that with HOI addition. B: Under random node removal, the empirical web (orange bars) and the totally random networks (grey, left) are not significantly changed by the addition of HOIs; while small-world (grey, middle) and scale-free networks (grey, right) loose robustness under HOI addition.

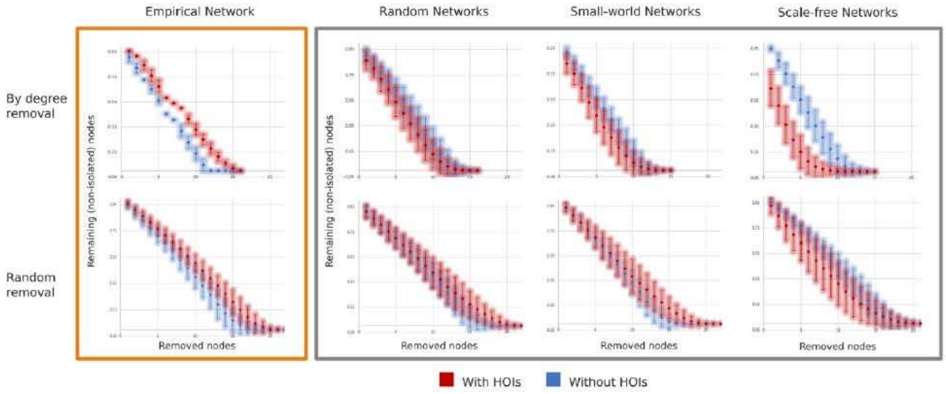

Fig. 6. Proportion of remaining nodes after sequential node removal and secondary extinctions. Left (marked in orange): empirical networks. Right (marked in gray): randomized networks. Above: Random node removal. Below: By degree node removal. In red we show the data of the networks with HOIs or similar general structure and in blue we show the data of the networks without HOIs or similar general structure. Each dot is the average of 200 networks and vertical shadows are standard deviations. HOI addition in the empirical networks (left) result in a slower diversity decline, while randomized null models (right) show the opposite or no tendency. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

associated network that includes both simple and high order ecological interactions (Fig. 3). This network has enabled us to test the role of HOIs on the network's robustness for a system of great ecological and agricultural importance. We find that the robustness of the coffee-associated network structure, measured through an operational index and through a secondary extinction analysis, is unchanged or increased by HOI addition, and that random reconfigurations indicate that this effect is not simply due to edge addition (Fig. 5 and 6). This goes in agreement with previous studies considering hypothetical networks and different measures of system function like stability or feasibility, where the addition of simple interactions has been found to have negative repercussions on system function while HOI addition has a neutral or a positive effect (May 1972; Bairey et al., 2016; Grilli et al., 2017; Singh and Baruah, 2020; Li et al., 2020). Our results therefore support the idea that HOIs contribute to the maintenance of highly diverse ecological communities.

In our study, the robustness of the network was first evaluated with the change in size of the biggest connected component as the nodes were gradually removed, at random or by targeting nodes of higher degree first. This way of conceptualizing robustness assumes that the connection between network components is related to the function and integrity of the system, implying that a fully connected network can maintain its elements and overall functions better than a disaggregated or partially disconnected network (Albert et al., 2000; Dekker and Colbert 2004; Piraveenan et al., 2013; Sheykhali et al., 2020). Indeed, previous work on the coffee agroecosystem for which the network under study has been uncovered suggests that some agroecosystemic functions, such as pest control, rely on the dynamics of the whole system and on the documented interactions taking place (Vandermeer et al., 2010). In the particular case of agroecosystems, the integrity of the network, in other words the maintenance of its diversity, is also likely to be associated with yield and yield stability in the face of diverse perturbations

(Gaudin et al., 2015; Manns and Martin 2018). Additionally, we strengthened our analysis with a direct quantification of secondary extinctions along the primary node removal sequence. In this case, the assumption is simply that species loss results in co-extinctions whenever it leaves other species isolated. This second approach confirmed our results, supporting the idea that HOIs increase the robustness of the system and that the robustness index that we used is a good measure of the overall state of the system.

The node removal methods that we used have been explored in many ecological network studies, and our results confirm the general tendency of ecological networks to be less robust to directed loss of the most connected species than to random species loss (Dunne et al., 2002; Kaiser-Bunbury et al., 2010; Roopnarine 2010; Cai and Liu 2016). Thus, it is remarkable that under directed node removal, HOI addition bears the larger positive influence on robustness. While the extinction of the most connected species in most communities might be unlikely, given that they are often the most abundant ones (Dáttilo et al., 2014;Vázquez et al., 2005; Vázquez et al., 2007), we should bear in mind that we are dealing with an agroecosystem, which by definition if human-managed and which can be subjected to directed emotions (for example, in the case of pests). These intentional removals may very well be directed to largely abundant species, making the study of directed node removal all the more relevant.

While the coffee-associated system was studied here as an undirected network, the type and sign of its HOIs could inform the mechanism through which HOIs affect the overall robustness. For example, in this ecological system all documented HOIs are negative, meaning that they work as inhibitors of the ecological interaction they modify, thereby diminishing their intensity (although they sometimes form double negatives, as third order interactions inhibit previous inhibitions, amounting to a general positive effect). This may have several implications for the system's dynamics. For example, refuge provisioning, where one species protects another from one or several predators, may not only help explain prey survival (which is important for maintaining the predator), but also how predators avoid competitive exclusion (Vandermeer and Perfecto 2019). It is possible that these mechanisms, coupled with spatial and temporal heterogeneity, may create the necessary conditions for coexistence. However, it is important to bear in mind that individual HOIs may have effects in different directions. Especially in the case of agroecosystems, where effects are measured also in terms of human-based values like productivity, the effect of individual HOIs should not be universally assumed as positive. For instance, it has been shown that the ant *Wasmannia auropunctata* can indirectly protect the coffee leaf miner against potential predators, potentially limiting the effectiveness of biological control elements (Perfecto et al., 2021). Nevertheless, we could not compare the effects of positive and negative HOIs in this study as we worked with undirected networks, such a question remains an interesting pathway for future research.

The structural analyses of the coffee-associated network also allowed us to identify nodes with high centrality according to different metrics (Fig. 4). We identified five nodes that systematically exhibited a high centrality, independently of the centrality measure and the presence or absence of pseudo-nodes: *C. viridis, Coffea, H. hampei, Azteca, Pheidole* ctp. and *Pseudomyrmex* spp. This is in agreement with the crucial role of the coffee plant in this agroecosystem, as well as the effect of its potential pests and pest enemies in its growth and development (Vandermeer et al., 2010). However, at this point we cannot rule out the possibility that the high centrality of these nodes is due to a bias in sampling and research efforts. We therefore cautiously interpret the results on node degree and betweenness centrality; rather than highlighting specific nodes as potential keystone species or indicators, we used these metrics mainly to characterize the overall structure of the network and found that the high centrality of these nodes was generally unaltered by pseudo-node addition, which suggests that this method for representing HOIs is able to conserve key aspects of the network.

A key assumption in our analysis is that robustness depends upon network structure, a simplification that does not take temporal dynamics into account. The relationship between structure and function in networks is certainly unclear and remains an active and open field of research, with key questions largely unexplored. However, there is an important body of literature on this matter, from which some structural metrics and robustness analyses like the ones we used have emerged as potential indicators of network functioning and dynamics. For instance, computational and empirically-based studies on social-ecological systems have employed purely structural measures in order to identify nodes that can lead to large cascading effects, as well as potential indicators of overall system integrity (see for recent examples: Kaiser-Bunbury et al., 2010; Lü et al., 2016; Cai and Liu, 2016; Griffith et al., 2019; Horcea-Milcu et al., 2020; Puche et al., 2020; Cagua et al., 2019; Arroyo-Lambaer et al., 2021; Gouveia et al., 2021; Yang et al., 2021; Zamkovaya et al., 2021, among many others). Hence, even though the study of network structure alone cannot account for temporal phenomena, it has proven to be useful and valuable in its simplicity. On the other hand, dynamical approaches contribute with an important and complementary perspective, and there are novel methods being actively developed that promise to enrich our understanding of robustness in ecological systems (Neubert and Caswell 1997; Arnoldi et al., 2016; Saavedra et al., 2017; Saavedra et al., 2020). We are currently pursuing dynamical analyses that might help uncover the role of HOIs and highly central nodes on the dynamics of populations in the coffee-associated network. With these, we expect to be able to discuss the scope of the structural approach considered here in its relationship to spatial-temporal dynamics. Studies have historically found different relationships between the amount and type of interactions in a network and several measures of its stability and robustness (see Landi et al., 2018 for a thorough revision on this matter). Hence, complementing the present study with a dynamical analysis will allow us to get a more realistic vision of the system and what the consideration of HOIs may or may not entail.

To conclude, our results support the hypothesis that HOIs can contribute to the maintenance and robustness of highly diverse ecological systems, and agroecological systems in particular. In agreement with previous empirical and theoretical studies, our work points to the importance of agroecological management and practices that are based on a deep ecological understanding of productive systems, as well as to the importance of a high diversity of taxons and interactions for the robustness and functioning of agroecosystems.

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Author statement

All authors declare that they have seen and approved the final version of the manuscript being submitted. They warrant that the article is the authors' original work, that it hasn't been previously published and that it is not under consideration for publication elsewhere.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecocom.2021.100951.

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CAPÍTULO III

EFECTO DE LAS INTERACCIONES DE ALTO ORDEN EN LA DINÁMICA DE LA RED DEL CAFETAL

PREFACIO

Como hemos venido discutiendo, las interacciones de alto orden prometen ser un mecanismo importante mediante el cual las especies se afectan unas a otras, y mediante el cual las comunidades logran sostener la alta diversidad que en muchos casos observamos. Sin embargo, esto aún está poco estudiado y para hacer generalizaciones, es importante contar con evidencia desde muchos sistemas de estudio, tanto teóricos como reales y desde muchas metodologías. En el capítulo anterior presentamos el efecto de las interacciones de alto orden en la robustez de la estructura de una red empírica de un agroecosistema cafetalero. En él concluimos que las HOI tienen un efecto positivo o neutral sobre la red en cuestión, desde la perspectiva de su robustez ante la pérdida de nodos. Mientras que éste es sin duda un resultado sugerente, debemos considerar que analizar la estructura de las redes es sólo una aproximación de las muchas posibles, y que para ser congruentes con lo que hemos venido discutiendo en este manuscrito, debemos complementar este análisis con otras metodologías.

Con los estudios de redes podemos, además de analizar la estructura de los sistemas, dotarlos de una dinámica temporal. Para ésto, representamos el estado de los nodos (o de las aristas en algunos casos) a través de modelos matemáticos de varios tipos, discretos o contínuos, como los modelos booleanos o las ecuaciones diferenciales que representan las densidades poblacionales de los diferentes componentes de la comunidad (Gaucherel et al. 2017; Diz-Pita y Otero-Espinar 2021).

Las redes tróficas extendidas, como lo vimos en el capítulo I, son una manera de integrar todo tipo de interacciones ecológicas en sistemas que se basan en ecuaciones diferenciales de tipo consumidor-recurso. En particular, las interacciones de alto orden se pueden incorporar a estos modelos al definir la interacción entre dos especies en función de la densidad de una tercera especie. De este modo, modificando los distintos términos de la ecuación de nuestra elección, podemos representar una infinidad de casos donde algún fenómeno se ve modificado por otra especie. Sin embargo, para modelar una comunidad biológica de esta manera, no basta con definir sus ecuaciones, sino que también es necesario parametrizarlas.

Debido a lo difícil que es contar con parámetros empíricamente obtenidos para cada especie e interacción específica a modelar, muchas veces se han utilizado parámetros aleatorizados. Este método sacrifica especificidad pero ofrece una mirada general útil para poner a prueba muchos principios en la ecología. Por otro lado, en una posición intermedia entre lo aleatorio y lo exacto, se encuentra una forma de parametrizar llamada “modelo bioenergético”, originalmente desarrollado por Yodzis e Innes (1992). Éste permite establecer los parámetros en ecuaciones de tipo consumidor-recurso basándonos en el tipo de organismos que queremos modelar (vertebrados, invertebrados, microorganismos), su nivel trófico y su tamaño corporal. A lo largo de los años se ha seguido desarrollando y es hoy una de las mejores herramientas con las que contamos para parametrizar ecuaciones cuando no contamos con medidas empíricas específicas para cada especie y cada interacción, pero deseamos un análisis más apegado a la realidad de lo que puede brindar una aproximación aleatoria.

Con base en lo anterior, en este capítulo presentamos un análisis dinámico de la red asociada al cafetal que es nuestro sistema de estudio. La modelamos mediante una red trófica extendida para incorporar interacciones de alto orden y la parametrizamos de acuerdo al modelo bioenergético (Hale *et al.* 2020; Glaum *et al.* 2020; Brose *et al.* 2006; Yodzis e Innes 1992). Con este modelo, realizamos dos experimentos. En el primero eliminamos nodos paulatinamente de manera aleatoria tanto en la red completa como en una versión de la red que carece de interacciones de alto orden y en ambos casos comparamos la supervivencia de las especies y la abundancia de algunas especies clave. En el segundo experimento eliminamos aleatoriamente, por un lado, las interacciones de alto orden, y por otro, las interacciones de primer orden. Comparamos el efecto de perder estos tipos de interacción sobre la supervivencia de las especies y sobre la abundancia de algunas especies clave.

En general, encontramos que ante la pérdida de nodos, las interacciones de alto orden no tienen un efecto significativo sobre la supervivencia de las especies en la red ni sobre las abundancias de algunos nodos clave. Por otro lado, mientras que la remoción de interacciones de primer orden tiene un efecto negativo sobre la supervivencia de las especies, la remoción de interacciones de alto orden tiene un efecto positivo. Los experimentos de este capítulo fueron diseñados especialmente para dialogar con lo que encontramos en el capítulo II, pero mientras que en dicho análisis las HOI demostraron tener un papel ligeramente positivo o neutral sobre el funcionamiento de la red, en el presente capítulo jugaron un papel neutral. En vista de esto, concluimos que es necesario realizar más estudios con diferentes sistemas biológicos y con diferentes aproximaciones metodológicas para determinar la relevancia de las interacciones de alto orden en el funcionamiento de las comunidades biológicas.

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Effects of high-order interactions in the dynamical modeling of an agroecosystem network

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ABSTRACT

High order interactions (HOIs) are increasingly being studied as a crucial feature of ecological communities, as they are ubiquitous in nature and their effects can be profound. Moreover, it has been suggested by both hypothetical and empirically informed models that HOIs may be important for promoting the existence of highly diverse systems. In a diversified coffee system in Chiapas, Mexico, observations and field experiments have also suggested that this kind of interactions are partially responsible for the persistence of the system and the autonomous regulation of its potential pests. Here, we modeled the interaction network of 22 of the best documented species in this coffee system. We tested whether the inclusion of HOIs is important to the overall performance of the community in the face of species loss, measured as mean species survival and abundance of some key components. To this end, we used the framework of extended food webs, parametrized according to the bioenergetic model, which is based on allometric relationships between species. We found that HOIs presence did not result in significant differences in species survival or abundance. While specific HOIs may have very important ecological effects, this study provides no evidence of a general positive or negative role of HOIs in species survival rate or abundance. These findings are in line with a previous study of the same network, which from a purely structural point of view, found that HOIs had positive or neutral effects on the robustness of the network under different perturbations. Further studies are still necessary in order to gain a nuanced understanding of the role of HOIs in agroecosystems and ecosystems in general.

Keywords: Ecological networks, High order interactions, Species coexistence, Coffee agroecosystems, Dynamical modeling, Extended food web, Bioenergetic model

1. Introduction

One of the most active fields in theoretical ecology has been that which seeks to explain the coexistence of organisms in highly diverse communities (Valladares et al. 2015). The interactions that organisms have with each other are the spinal cord of these systems, and as such, they have been at the center of these investigations. Through the decades, we have learned much about the way in which communities are structured and how different kinds of interactions, such as competition, predation, and mutualism, shape their dynamics or their functions. Recently, a new way in which organisms relate to each other through the so-called high order interactions (HOI) has been increasingly studied. HOIs occur when the interaction between two species is modulated by a third species, without this necessarily happening through changes in population densities (Billick & Case 1994). HOIs are increasingly regarded as a crucial part of ecological dynamics, as they occur widely in nature and they can profoundly affect organisms. Additionally, some theoretical studies have suggested that they may play an important role in allowing communities to harbor numerous species (Bairey et al. 2016, Battiston et al. 2021). Nevertheless, the effects of HOIs on the diversity of communities and on interaction networks (e.g., how strongly they affect first order interactions, interaction strength, connectivity, clustering, etc.) is still unclear.

Studying the effect of HOIs on community structure or diversity requires a well-known system with well-documented interactions. Such networks are scarce, but one of them can be found in a coffee agroecosystem in Chiapas, Mexico. This system has been studied for over twenty years, producing knowledge about many of the species it harbors and their interactions On this site, a set of high order interactions have been studied for their possible role in maintaining biodiversity and sustaining an autonomous pest regulation system (Vandermeer et al. 2010; Perfecto & Vandermeer 2015). Recently, this network has been updated with new empirically recorded first and high order interactions among 22 taxa (González et al. 2021, Figure 1). Based on this updated network, an analysis of its architecture showed that HOIs made the network more robust to random node removal. However, HOIs showed no effect when nodes were removed in a targeted way, from highest to lowest degree. In this analysis, robustness was measured as the rate at which the biggest connected component grew smaller as nodes were removed. While this work pointed to HOIs as likely important for species persistence, it focused on the structure of the network and not on its possible dynamics. Because different formalisms and modeling strategies often reveal or hide different phenomena, the effect of HOIs on interaction networks needs to be tested through diverse modeling approaches. In this study, we examine how HOIs affect species survival and abundance by modeling the dynamics of populations in the network, an approach that seeks to complement previous efforts aimed at understanding the role of HOIs in biological communities.

The dynamical modeling of ecological species populations has a long history, from Lotka-Voltera equations designed for a single type of interaction, like predation or competition, to more complex models that integrate different kinds of interactions and the fine-grain mechanisms by which these happen (MacArthur 1970; Yodzis & Innes 1992; Brose 2008). The inclusion of several species in such equations has always proven difficult, since chaotic behaviors usually arise as the number of species increases, causing the simulated systems to often collapse. Nevertheless, decades of studying and fine-tuning these models have allowed researchers to study systems containing tens of species, and sometimes more than a hundred (Kefi et al. 2016; Landi et al. 2018). This has opened the door for ecologists to test hypotheses and ask further questions, while working with real-world and diverse ecological communities (Kefi et al. 2016; Williams & Martinez 2004, Glaum & Valdovinos 2020; Hale et al. 2020). As a result, the knowledge on what maintains diverse biological systems is growing, and we are getting a better grasp on the role that different elements play on the persistence and resilience of ecosystems (Landi et al. 2018). In this context, HOIs seem to be crucial, although the best way to represent them in models is still an open question (Bairey et al. 2026; Golubski et al. 2016; Battiston et al. 2021).

Here, we modeled the ecological network of a coffee-producing system (Figure 1) with resource-consumer equations that were modified to include first, second and third order interactions. As far as we know, this is the first use of this approachto study HOIs in the context of a real world agroecosystem. We seeked to examine the effect of HOIs in this system, aiming at a better understanding of the functioning mechanisms of this very ecologically and economically important agroecosystem. Coffee is a commodity that is consumed worldwide and, because of its ecological requirements, it is produced in highly biodiverse regions. As a result, it is embedded within ecosystems that are crucial in terms of biodiversity conservation (Moguel & Toledo 1999). Coffee farms are represented by a wide range of management strategies spanning from systems that are as diverse as primary tropical forests to monocultures with very low biodiversity (Perfecto & Vandermeer 2015). Additionally, coffee agroecosystems are also important for the livelihoods of millions of families that depend on one or more of the stages of its productive process, and which are in many cases peasants or indigenous peoples, some of the most economically vulnerable groups in our society (ENA 2017; SAGARPA 2017). Thus, understanding the mechanisms that drive the dynamics of this agroecosystem is crucial both from an ecological and an economical point of view. In this sense, understanding the role of HOIs may not only add to ecological theory, but it might also inform management strategies promoting coffee production and biodiversity conservation simultaneously. Given that HOIs are ubiquitous in nature and that they might help highly diverse communities to persist, studying them through dynamical modeling will likely help us to understand their relevance and point to the mechanisms through which they operate.

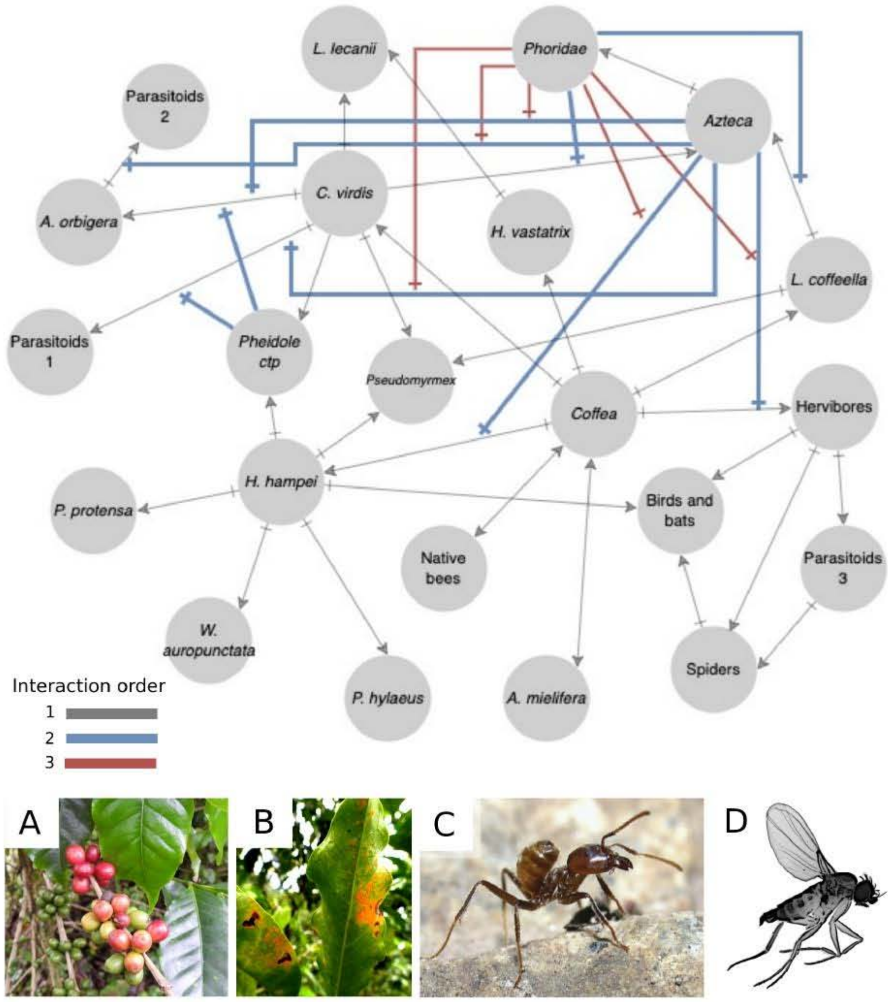

Figure 1. Up: Community network with first (gray), second (blue) and third (red) order interactions. Line endings represent positive effects, crossed endings are negative effects, and simple endings represent no effects. A: Coffee plants. B: Coffee Rust. C: *Azteca* ant. D: *Phoridae*.

2. Methods

2.1. Study site and network

The study site is “Finca Irlanda”, a 320 ha coffee plantation situated on the highlands of El Soconusco, Chiapas (158,110 N, 928, 200 W; 900 masl). Precipitation in the region averages 4500 mm per year and the primary vegetation is tropical montane rainforest. In the study region, the original vegetation has been almost completely replaced by coffee plantations with different management intensities, aside from forest fragments that are conserved in some farms. Finca Irlanda conserves patches of rainforest surrounded by coffee plantations shaded by native trees, which, in combination with the use of organic compost and no pesticides or herbicides, make Finca Irlanda a highly biodiverse agroecosystem (Perfecto et al., 2004). This system has been very well documented in terms of species interactions including first, second, and third order interactions (Fig. 1) making it ideal for the study of the role of HOIs in ecological community function.

In this site, the ecologic network involves plants, insects, fungi, birds and mammals. First order interactions include predation, herbivorism, pollination and parasitoidism. The documented second and third order interactions consist of inhibitory phenomena where the presence of one species cancels the lower order interaction between other species. For example, the *Azteca instabilis* ant nests in several shade trees along the coffee plots. These ants maintain a mutualistic relationship with the green coffee scale, which they protect from natural enemies in exchange for the honeydew the scales produce. High order interactions occur when the ants patrol the coffee plants where scales conglomerate and attack any natural enemy they encounter, like parasitoids or predators of the scales. These are high order interactions because *Azteca* does not necessarily kill the enemies, rather, it pushes them off the coffee plant and deterrs any further exploits. By doing this, the ants not only protect the scales, but also the coffee plants themselves, because they do not make distinctions while patrolling. These are second order interactions because they modify (inhibit) first order interactions such as parasitoidism on green scales or herbivory on coffee. Nevertheless, these second order interactions are also modified by a third order interaction: flies from the family Phoridae (genus *Pseudacteon*) are parasitoids of *Azteca* ants, ovipositing in their bodies and causing their heads to fall off when the larvae emerges. *Azteca* ants change their behavior when they sense a phorid fly nearby and hurry back to their nest or stay completely still. Hence, when phorids are around, the second order interactions that *Azteca* normally maintains get temporarily inhibited, allowing natural enemies of coffee and green scales to act. This intricate network has been understood as an autonomous pest control system, because it allows for the survival of many species, some of them potential coffee pests, but keeps their populations below economically problematic thresholds through the action of these and many other interactions of distinct types and orders (Vandermeer et al. 2010). Documenting and studying these interactions is far from trivial, and models such as the one we present are a valuable tool to discuss their effects.

2.2. Equation: extended food web

We modeled this system using the framework of “extended food webs” (García-Callejas et al. 2018). In this framework, trophic interactions are considered as the backbone of community dynamics, which are modeled through ordinary differential equations. Non-trophic interactions are included as functional modifiers of the kinetic equation’s parameters, for example, reproduction, migration or attack rates, according to the specific mechanism by which species interact with each other (for more information on extended food webs and similar frameworks, see García-Callejas et al. 2018, Arditi et al. 2005; Kefi et al. 2012). Importantly, a HOI can be introduced by making the parameter which describes the interaction between two species a function of the population density of a third interacting species.

We wrote a set of differential equations to model the population dynamics of the nodes of the network and studied the role of HOIs on species survival and abundance in the face of perturbations. Following Kefi and collaborators (2012, 2016), Eq. (1) reads as follows:

$$\frac{dB_i}{dt} = r_i\left(1-\frac{B_i}{k_i}\right)B_i + e_i B_i \sum_j a_{ij}F_{ij} - \sum_j a_{ji}B_j F_{ji} - X_i B_i \tag{1}$$

where B_i is the biomass of species *i*, r_i is the intrinsic growth rate ($r_i > 0$ only for the primary producer, $r_i = 0$ for the rest), k_i is the carrying capacity, e_i is the conversion efficiency (the portion of the consumed biomass of species *j* that that is actually metabolized by species *i*), F_{ij} is the functional response, *a* is a *n* by *n* matrix where *n* is the number of nodes of the network and whose element with index *ij* is 1 if species *i* consumes species *j* and 0 otherwise, and X_i is the metabolic rate. The functional response F_{ij} is given by Eq. (2) as follows:

$$F_{ij} = \frac{w_{ij}B_j^{1+q}b_{ij}}{1+h_i\sum_k w_{ik}a_{ik}B_k^{1+q}b_{ik}} \quad , \qquad (2),$$

which is a Holling-type functional response for multiple prey (Holling 1959). In this equation w_{ij} is the relative consumption rate, which accounts for the fact that a single consumer eats several resources (w_{ij}= 1/ the number of resources of species i); b_{ij} is the attack rate of *i* on *j*; h_i is the handling time of predator *i*; 1+*q* is the Hill's exponent where q=0 corresponds to a type II response and q=1 to a type III response; here we used q=0.5, corresponding to a weak type III response and for which evidence shows more stable dynamics (Williams & Martínez, 2004; Glaum et al., 2020; Hale et al., 2020).

The non-trophic interactions in this system were included by modifying the parameters in Eq. (1). First order non-trophic interactions (pollination) were coded in a *POLIN* matrix of size *n* by *n* where the element with index *ij* is 1 if species *i* is pollinated by species *j*. Second order interactions, namely those mediated by refuge provision, were coded in the tensor *REF* of size *n* by *n* by *n*, where the element with index *hij* is 1 if the species *h* inhibits the predation of species *i* on species *j* (*h* provides refuge for *j*), and is 0 otherwise.

With these changes, the parameters in Eq. (1) are modified as follows. Improvements in coffee recruitment as a result of pollination were incorporated in the growth rate r_i, in such way that this parameter becomes a saturating function of pollinators biomass:

$$r_{inew} = \frac{r_i + r_{max}\sum_p POLIN_{ip}B_p}{1+\sum_p POLIN_{ip}B_p} \quad , \qquad r_{max} = r_i(1+random(0,1)) \tag{3}$$

Where p are the species that pollinate species i, r_{max} is the maximum growth achieved in the presence of pollinators and *random(0,1)* is a uniformly distributed random number between 0 and 1.

Refuge provision was incorporated in the attack rate b_{ij}. Refuge provision has been taken into account in previous studies but has not been understood as a second order interaction, as it was considered as a positive effect of species *r* on species *j* rather than an inhibition on the interaction *ij* (Kefi et al., 2016). There is an important difference between these two conceptualizations, as the first one assumes that the effect of species *r* on *j* is independent of the predator *i*, in other words, *r* protects *j* from all its predators. While this may be sometimes the case, an *rij* interaction allows us to consider each possible interaction *ij* separately. While in our case the first option may suffice, we believe that the second option is more general and includes the first one. For instance, the case where *r* actually protects *j* from all predators is a specific case of a second order interaction. From a conceptual point of view, the interaction *rij* is an effect of *r* on an interaction, hence a second order interaction, and an interaction *rj* is an effect or *r* on a node, hence a first order interaction. Lastly, B_r was divided by a factor λ = (0.5, 0.05) in order to enhance the effect of refuge provision in the face of small population densities. Thus, the attack rate b_{ij} was modified as follows:

$$b_{ijnew} = \frac{b_{ij}}{1 + \sum_h REF_{hij} \frac{B_r}{\lambda}} \tag{4}$$

Where *r* are the refuge provider species.

To include third order interactions into an attack rate, which in this case represent Phoridae inhibiting refuge provision, the following expression is used:

$$b_{ijnew} = \frac{b_{ij}}{1 + \frac{\sum_h REF_{hij} \frac{B_r}{\lambda}}{1 + \frac{B_{phoridae}}{\lambda}}} \tag{5}$$

This form incorporates a saturation function depending on the population of Phoridae. $B_{phoridae}$ was also divided by λ = (0.5, 0.05) in order to accentuate the effect of third order interactions.

2.3. Parametrization: bioenergetic model

The parameters for the equations presented above were determined according to the bioenergetic model originally developed by Yodzis and Innes (1992) and further improved by many authors (Williams & Martínez, 2004; Brose et al., 2006; Brose, 2008; Williams, 2008; Stouffer & Bascompte, 2010; Stouffer & Bascompte, 2011; Kefi et al., 2016; Hale et al., 2020; Glaum et al., 2020). The purpose of this general model is to provide plausible consumer-resource models based on the allometric relationships between organisms production rates, metabolism and consumption. Metabolic constants have been derived empirically for several organism types (endotherms, vertebrate ectotherms, vertebrate endotherms, invertebrates, plants, and microorganisms). Coupling these constants with the trophic level of species, the parameters of the equations can be determined when no specific rates have been measured for the organisms in question. Table 1 shows the parameters used in this model as well as the initial conditions employed.

Table 1. Parameters used in the model. Parameters were estimated following a bioenergetic approach, as in Hale et al. (2020), Glaum et al. (2020), Kefi et al. (2016).

Parameter	**Definition**	**Value**
m_i	Biomass of species *i*	$m_i=Z^T$ where T is the trophic level (starting from 1 for herbivores and up to 4) and Z= 10 for invertebrates and fungi and Z=100 for vertebrates. m_i of the primary producer =1.
r_i	Intrinsic growth rate	r_i=1 for the primary producer, r_i=0 for the rest
K_i	Carrying capacity of species *i*	1 for all
e_i	Conversion efficiency	0.85 for carnivores, parasitoids, *L. lecanii* and *Azteca*, 0.45 for herbivores and *H. vastatrix*
x_i	Metabolic rate of *i*	0 for the primary producer and x_0*m_i^(-0.25) for the rest, with x_0 a randomly chosen number between 0.1 and 0.5
w_{ij}	Relative consumption rate of *i*	1/(number of resources *i* consumes)

b_{ij}	Attack rate of predator *i* on prey *j*	x_i *(y_i/B_o) y_i is the maximum consumption rate, y_i=8 for invertebrates and fungi, y_i=2 for vertebrate endotherms B_o=0.5, which is half the saturation density
h_i	Handling time for predator *i*	1/(y_i* x_i)
1+q	Hill's exponent	q=0.5 (weak type III functional response)
B_i	Initial populations	random abundances distributed in the interval [0.1,1]

The model and all numerical experiments were implemented using the *HTCondor* software and were coded on *Python 3.7.1.* The codes are available at: https://github.com/laparcela?tab=repositories.

2.4. Numerical experiments

Once the dynamical model for the network was defined, we carried out three experiments. In the first one, we subjected the system to random *node* removal and compared its performance with and without HOIs. That is, we ran two versions of the model, the first one included all HOIs and the second was deprived of HOIs by setting the *REF* tensor to zero. In both versions, we eliminated randomly selected nodes one by one, and at each step of node removal we ran the population model with the same initial conditions for 1000 time-steps to reach the steady state according to our manual revision. As response variables, we measured the proportion of surviving species and the abundance of coffee, the potential pest coffee rust, and the *Azteca* ant involved in pest control. Besides being relevant in productive terms, these species correspond to the nodes with the highest centrality values in the network (González et al. 2021). Survival at each node removal step was measured as the proportion of species left alive after the 1000 time-steps, where a species was considered extinct if its abundance went below 0.000001. The experiment was carried out on 200 independently generated initial conditions and we report the averaged results across all simulations.

Then we conducted a second experiment which differed from the first one in that the nodes were removed following a descending order of degree. That is, the nodes were removed from the most connected to the least connected ones. Where two or more nodes had the same degree value, the order amongst them was selected randomly. The other details were identical to experiment number one.

In the third experiment, we took the complete system and subjected it to two kinds of *interaction* removal. On the one hand, we randomly removed first order interactions one by one. On the other hand, we randomly removed high order interactions one by one. Like in the previous experiment, we ran the population model for 1000 time-steps after each interaction removal. We compared the effects of these two kinds of perturbations on the proportion of surviving species and the abundances of the same key species as before (coffee, coffee rust and *Azteca* ant). This experiment was also performed on 200 independently generated simulations and results were averaged across them.

3. Results

Figure 2 shows that in experiments where nodes were removed, either in a descending order of degree (A) or randomly (B), the average species survival did not differ significantly in networks with and without HOIs. This means that under our modeling conditions, the inclusion of HOIs had no effect on the proportion of species that survived. In addition, the response of mean species survival to node remotion was not linear, as both curves show a non-monotonous behavior. In contrast, in experiments where interactions were removed (C), the removal of first order interactions caused a constant decline in mean species survival, whereas HOI removal caused a linear increase in mean species survival. Standard deviations had a similar behavior across experiments.

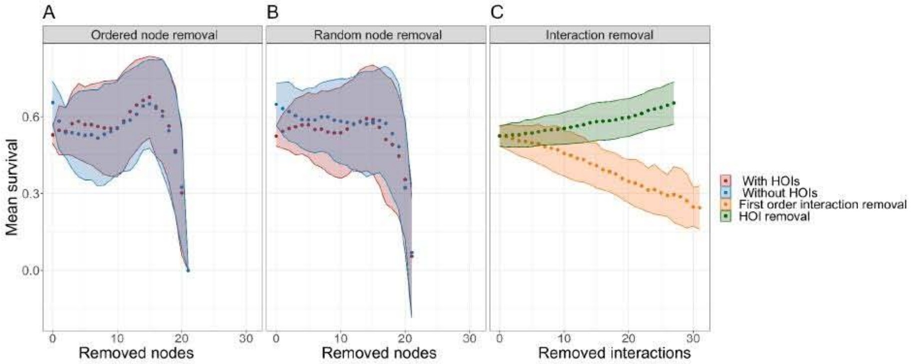

Figure 2. A: Mean species survival (where 1 means that all species in the community survived and 0 that none did) as nodes are removed one-by-one in a descending order of node degree. B: Mean species survival as nodes are randomly removed one-by-one. C: Mean species survival as interactions are randomly removed one-by-one. In A and B, red dots represent simulations performed in networks where HOIs are included and blue dots represent simulations where HOIs are not included. In C, orange dots represent networks where first order interactions were removed and green dots represent networks where HOIs were removed. Vertical lines are standard deviations and λ=0.05.

Figure 3 shows that key species abundances also had a different response to random node removal (top graphs) compared to random interaction removal (bottom graphs). With random node removal, the average abundance of the three key species dropped, although there were no differences between networks with and without HOIs. On the other hand, under random interaction removal, the average abundances of the three species remained almost unaltered, and again there were no significant differences between networks where HOIs were removed and networks where first order interactions were removed. Standard deviations differed a lot more between these two groups, since they were larger for networks where first order interactions were removed. Graphs corresponding to ordered-by-degree node removal are not shown since the three species have a high degree and hence get removed too soon in the simulations; they can be found in the supplementary material, along with the graphs for λ=0.5 and plots where simulations are not averaged. Those results all show the same tendencies as in Figures 2 and 3.

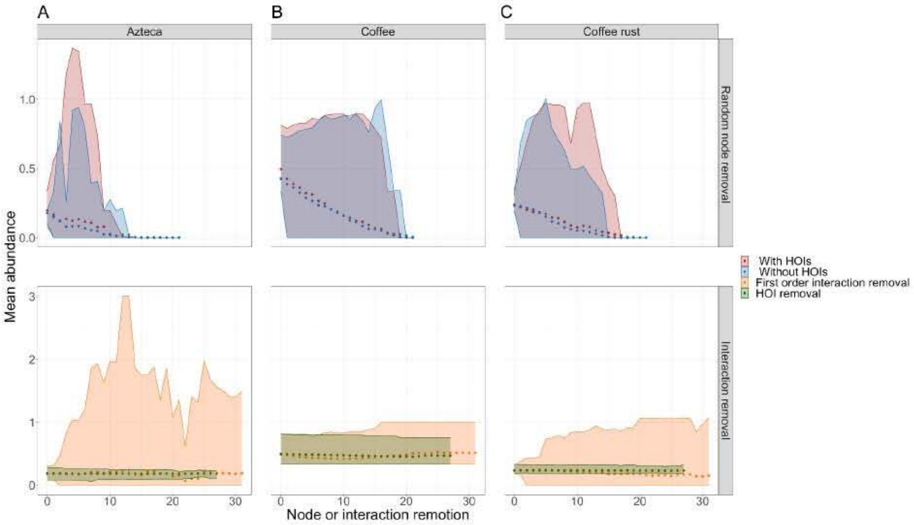

Figure 3. A: Mean abundance of *Azteca* ant as nodes are randomly removed (top) and as interactions (bottom) are randomly removed one-by-one. B: Mean abundance of Coffee as nodes are randomly removed (top) and as interactions (bottom) are randomly removed one-by-one. C: Mean abundance of Coffee Rust as nodes are randomly removed (top) and as interactions (bottom) are randomly removed one-by-one. In the top graphs, red dots represent simulations performed in networks where HOIs are included and blue dots represent simulations where HOIs are not included. In the bottom graphs, orange dots represent networks where first order interactions were removed and green dots represent networks where HOIs were removed. Vertical lines are standard deviations. Colored shadows represent confidence intervals (prob=0.025). We set λ=0.05 in all figures.

4. Discussion

Understanding the mechanisms that drive and allow for the coexistence of species is crucial in terms of biodiversity conservation, but it can also be enlightening in terms of the management of agroecosystems. In this context, the present study found no significant effects of HOIs on the proportion of species in the community that survived or on the abundances of some key species. This is in contrast with other studies, which have found positive effects of HOI on variables such as survival, robustness or linear stability, in both hypothetic and empirically derived systems (Kefi et al. 2012; Bairey et al. 2016; Grilli et al.

2017; Terry et al. 2019). Nevertheless, in a recent study by Shen et al. (2023) on aquatic protists, HOIs were found to be important for the survival of only one of the five species they investigated, and only in one of the investigated scenarios, while first order interactions seemed to play a much more important role overall.

The known HOIs of our study system, even though they slightly change the trajectories of each species in each individual simulation, might not be strong enough to cause an effect on survival or even on the mean abundances at a community level. It is important to notice that HOIs in this system act differently for different species. Second order interactions have a positive effect on some species and a negative effect on others, while third order interactions have the opposite effect because they inhibit second order interactions. This could lead them to cancel each other out. In a previous study, in which we tested these same conditions from a purely structural perspective, HOIs only had an effect when nodes were removed by order of degree, and they showed no effect when they were randomly removed (González et al. 2021). Nevertheless, in this study, HOIs had no positive effect under any removal sequence. This would mean that, even though HOIs may have important effects for specific elements, we should not rush to generalize about their positive or negative nature for the community as a whole. Rather, they might only have specific effects under certain circumstances. Indeed, in Figure 2, it is evident that removing nodes leads to a general decline in survival. However, the significant drop occurs only when a majority of the nodes have been removed, a result that is quite obvious. Of greater significance, this figure shows that survival throughout the majority of the process exhibited a non-monotonic pattern without a consistent directional trend. This supports the idea that the effects of species and their interactions on the overall system cannot be generalized, rather, they have both positive and negative effects on different species. This highlights the need to be cautious about making general assumptions about the role of HOIs and on ecological interactions in general.

Additionally, we found that removing nodes had a qualitatively different effect on both survival and abundances than removing interactions. While node removal caused an overall drop on survival and abundances, interaction removal had almost no effect on abundances (except for standard deviations, which were much larger when first order interactions were removed) but a very marked effect on mean survival. Moreover, the effect on survival was positive for HOI removal and negative for first order interaction removal.

On a different line of thought, the lack of effect of HOIs under node removal could also be due to the limitations and assumptions of the modeling approach. The equation we used to represent the agroecosystem was parameterized according to the bioenergetic model, in a similar fashion as Glaum et al. (2020), Hale et al. (2020), Kefi et al. (2016). As we have said, this approach takes into account allometric relationships between organisms' traits in order to provide plausible parameters for each species, when empirical measurements are not available. This method has been widely useful, since field measurement of species rates is extremely difficult. Nevertheless, the model was first conceived for aquatic environments and it is best fit to represent them (Yodzis & Innes 1992). Allometric relationships between terrestrial species may not follow the same rules as aquatic species. For instance, marine predators almost always have considerably larger body sizes than their prey, a situation that is not prevalent in terrestrial environments, as in plant-consumer interactions where consumers are often smaller than the plant the forage on

(Shurin et al. 2006; Valdovinos et al. 2023). For instance, ants and spiders in our model system, which tend to predate on organisms at least as large as themselves, pose a challenge to this assumption. Also, organisms that are present in the network like fungi and parasitoids have not been explicitly studied for use with the bioenergetic model, so we had to make some decisions (see Table 1) to include them in the dynamical models that might not be entirely correct. Even though most organisms in the network do not present the latter problem, it remains a question whether better parametrization of these exceptions could render a model with more capacity for detecting the effects of HOIs. Both theoretical and experimental work is needed to adapt the bioenergetic model to this particular system and to terrestrial communities in general. Also, there is a great diversity of HOIs in ecology, but HOIs in this study are all related to refuge provision or its inhibition and they are observed in a small number of species. Incorporating other types and sources of HOIs in this system might change the outcome.

Finally, the methods developed here provide an open tool for future research. The network and the equations that model its dynamics are the product of decades of study and could be further improved and used to address many more questions. For example, adding a spatial dimension to this model could bring to light processes that are otherwise not visible. Understanding the ecology of agroecosystems is crucial for sustainability and we should study it from as many perspectives as we can. Understanding the role of species and the interactions they maintain can help us build and maintain both productive and biodiverse systems.

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CONCLUSIONES GENERALES

A lo largo de este trabajo, nos hemos cuestionado acerca de la contribución de las interacciones de alto orden al funcionamiento de las comunidades biológicas, abordando esta cuestión de manera simplificada al considerar el funcionamiento como la supervivencia de sus componentes. Para abordar esta indagación, proponemos la utilización del marco teórico de las redes ecológicas, donde definimos una red a partir de las interacciones empíricamente documentadas que sostienen un conjunto de especies asociadas al agroecosistema de un cafetal. Con esta red, llevamos a cabo simulaciones de escenarios que involucran la pérdida de especies y/o interacciones, analizando la contribución de las Interacciones de Alto Orden (HOI) a la supervivencia de la comunidad. Este análisis se realiza desde dos perspectivas: en primer lugar, examinamos la estructura de la red y su propensión a desconectarse; en segundo lugar, evaluamos la dinámica de los nodos mediante un modelo dinámico, observando su tendencia a extinguirse.

La revisión de literatura del capítulo I nos permitió entender la larga historia de investigación que ha tratado de ligar la estructura de las comunidades con su funcionamiento, y ubicar el estudio de las HOI dentro de esta tradición. Entendimos también que estos estudios muchas veces han llegado a conclusiones contrastantes, en parte debido a la complejidad de los sistemas vivos y en parte debido a las limitaciones de las metodologías empleadas. Por ello, entendimos la relevancia de abordar las preguntas desde la mayor cantidad de perspectivas posible. Discutimos cómo el uso de modelos y representaciones abstractas es necesario, y la importancia de entender las limitaciones de cada metodología, para lograr visiones integrales de nuestros objetos de estudio.

El capítulo II nos brindó una mirada a la estructura que las interacciones de alto orden generan en la comunidad de estudio y el impacto que tienen en su robustez. Los resultados apuntaron a que, en este sistema, las HOI tienen un efecto positivo o neutro en la robustez, entendida como la resistencia de la red a desconectarse conforme va perdiendo nodos. Esto significa que las HOI pueden ser importantes para que los ensambles biológicos se sostengan a través del tiempo y ante las posibles perturbaciones que enfrentan. Para complementar este resultado, en el capítulo III estudiamos esta misma relación pero dotando a la red de una dinámica poblacional. En este caso, no encontramos efectos de la presencia o ausencia de las HOI sobre la supervivencia de la comunidad ante la pérdida de nodos.

En conjunto, la evidencia generada en esta tesis sugiere que las HOI pueden tener un efecto positivo o neutro sobre las comunidades bióticas ante cierto tipo de perturbaciones. En el proceso de hacer este trabajo, aportamos al desarrollo de metodologías de estudio. Por un lado, propusimos un método para representar HOI en redes ecológicas simples, y un índice para medir la robustez de su estructura. Desde el punto de vista dinámico, este trabajo es el primero en utilizar una red trófica extendida en combinación con el modelo bioenergético para estudiar un agroecosistema, y explícitamente para incorporar HOI en su estudio. Creemos que los métodos aquí utilizados pueden ser de utilidad para estudiar otros sistemas y seguir ampliando nuestro conocimiento sobre el funcionamiento de las comunidades biológicas. Así mismo, estos métodos son parte de un esfuerzo continuo para crear modelos más integrales y por tanto es importante seguir mejorándolos y adaptándolos a diferentes sistemas de estudio.

Finalmente, la red que construimos representa un objeto de investigación valioso en términos de la investigación en Ecología, y en particular de los agroecosistemas. Como dijimos, éstos no sólo tienen una alta importancia ecológica sino también social, y sin embargo han sido mucho menos estudiados que los ecosistemas en general. Este trabajo nos permitió sistematizar y resumir la información de décadas de estudios en un solo objeto con el que se puede abordar un sinfín de preguntas. En resumen, hicimos una primera exploración de la importancia potencial de la diversidad de interacciones de distintos órdenes para el funcionamiento de la comunidad, y ubicamos elementos que desde el punto de vista estructural parecen ser clave. El conocimiento profundo de los mecanismos que operan en los agroecosistemas constituye la piedra angular del manejo sostenible. En consecuencia, la formulación de preguntas como éstas se vuelve esencial para construir sistemas productivos alineados con la conservación de la biodiversidad.

CONCLUSIONES PARTICULARES

CAPÍTULO 1

- Los estudios con redes ecológicas han sido muy utilizados para entender las relaciones entre la estructura y el funcionamiento de las comunidades.
- La diversidad de métodos y definiciones con que son estudiadas las relaciones estructura-función y las limitaciones de cada uno., generan resultados variables y en ocasiones contradictorios.
- Existen métodos nuevos que buscan subsanar las principales limitaciones de los métodos tradicionales.
- El espacio, el tiempo y los diferentes tipos de interacciones ecológicas generan dinámicas en los sistemas vivos que pueden analizarse con las nuevas metodologías en el estudio de redes: las redes multi-interacción y las redes con dimensión espacial y/o temporal.
- A la luz de estos nuevos métodos, las interacciones de alto orden parecen ser un aspecto importante de las comunidades que necesita seguir siendo estudiado.

CAPÍTULO 2

- Las HOI tienen un efecto positivo sobre la robustez de la red ante la pérdida de nodos en orden descendiente de grado.
- Las HOI no tienen un efecto sobre la robustez de la red ante la pérdida de nodos en orden aleatorio.
- La inclusión de HOI por medio de pseudo-nodos es un método útil para representarlas como redes clásicas y así poder utilizar todas sus herramientas de análisis.

CAPÍTULO 3

- Ante la pérdida de nodos, las HOI no tienen un efecto sobre la supervivencia de la comunidad ni sobre las abundancias de sus especies clave con este modelo.
- La pérdida de interacciones de primer orden tiene un efecto negativo sobre la supervivencia de las especies, mientras que la pérdida de HOI tiene un efecto positivo.
- Las redes tróficas extendidas son un método intuitivo para incluir las HOI en la modelación de interacciones bióticas y sus efectos sobre las poblaciones.
- El modelo bioenergético funciona mejor que el método aleatorio para parametrizar estas ecuaciones, pero es necesario adaptarlo a sistemas terrestres donde las relaciones biométricas que asume no siempre se cumplen.
- La incorporación de una dinámica espacial podría sacar a la luz efectos de las HOIs que en el modelo actual no son visibles.
- Es necesario seguir investigando las HOI para entender su papel en las comunidades y su importancia relativa respecto a otras características. Dicho entendimiento podría ayudarnos a diseñar estrategias sustentables de manejo de los ecosistemas.

PERSPECTIVAS

Este proyecto nos brindó una comprensión más profunda y detallada del estado actual del conocimiento respecto a las interacciones de alto orden y su potencial impacto en el funcionamiento de las comunidades. Además, nos condujo a la exploración de nuevas preguntas y propuestas experimentales. A continuación, destacamos los principales caminos de investigación que consideramos sería muy interesante recorrer.

Capítulo I: Este capítulo proporcionó una visión general del estado actual de los estudios de redes ecológicas, destacando las nuevas técnicas que se usan para abordar aspectos fundamentales de los sistemas biológicos. Dentro de este ámbito de investigación, se busca comprender los factores que llevan a cambios en el sistema, incorporando tanto variaciones temporales como espaciales. Tomando como ejemplo los agroecosistemas, factores como el manejo agrícola y la transformación de los paisajes pueden ser directa o indirectamente integrados mediante modificaciones en el estado de los nodos/aristas de las redes, o a través del modelado de redes acopladas en diversos espacios (consultar Apéndice V). La importancia de estos estudios radica en su capacidad para arrojar luz sobre las implicaciones de nuestras acciones en los ecosistemas, subrayando la necesidad continua de avanzar en la investigación en esta dirección y de sistematizar los resultados obtenidos en estas líneas de estudio.

Capítulo II: En este estudio, hemos construido una red que engloba a más de 20 especies, respaldada por evidencia empírica, en un tipo de agroecosistema de vital importancia tanto desde el punto de vista ecológico y social, como es el caso del cultivo de café. Consideramos que la propia red constituye un objeto de estudio continuo que requiere una exploración constante. Por un lado, proponemos la incorporación de nuevas especies e interacciones a medida que se profundiza en su estudio. Por otro lado, abogamos por analizarla mediante diversas técnicas y experimentos. En la actualidad, la red se centra principalmente en los invertebrados que interactúan con la planta de café. Para enriquecerla, sería esencial incluir el estrato arbóreo, arbustivo y herbáceo de la comunidad. Dado que el manejo de los cafetales determina de manera directa la diversidad de plantas mediante la adición o eliminación de especies en los diferentes estratos, contar con más especies vegetales en la red nos permitiría poner a prueba explícitamente el efecto de diferentes escenarios de manejo. En el ámbito de las HOI, surge la pregunta de cómo varían su efecto e importancia en contextos de manejo más o menos industrializados, planteando así una perspectiva valiosa para futuras investigaciones.

Capítulo III: En este capítulo, avanzamos en la aplicación de un modelo continuo para describir los cambios poblacionales de especies que interactúan a través de diversas formas de relación. Consideramos crucial continuar refinando este modelo, especialmente para adaptarlo de manera más precisa a los sistemas terrestres en general y al sistema de estudio específico. El modelo actual supone que las especies depredadoras siempre tienen tamaños corporales más grandes que sus presas, una premisa que funciona bien en ecosistemas acuáticos para los cuales fue originalmente concebido, pero que presenta limitaciones en entornos terrestres. Conviene, por ejemplo, pensar qué ocurre con los organismos parasitoides, que suelen ser mucho más pequeños que sus hospederos y sin embargo causan su muerte.

Además de ajustar los parámetros del modelo, consideramos que un siguiente paso para estudiar el sistema y el papel que juegan las HOI en él es dotarlo de una dimensión espacial. En algunos sistemas, ciertos factores parecen no tener efecto cuando se modelan sin considerar explícitamente el espacio, pero su importancia emerge al incluir esta dimensión (Dannemann et al., 2018; Vallespir Lowery & Ursell, 2019). A nivel local, las interacciones ecológicas se manifiestan cuando dos individuos se encuentran en el espacio, y a una escala más amplia, la estructura de las redes cambia según las especies presentes en áreas específicas. Por lo tanto, la inserción de la red en un contexto espacial nos proporcionaría una visión más precisa de la dinámica ecológica y permitiría estudios integrales a nivel de paisaje, donde diversas configuraciones de agroecosistemas coexisten en el espacio e interactúan con otros tipos de uso de suelo (ver Apéndices III, VI).

Finalmente, consideramos esencial explorar las HOI en otros agroecosistemas bien estudiados, como la milpa (López Martínez, 2017). Estos sistemas han evolucionado bajo la presión de la selección humana intencional, lo que no solo permite abordar cuestiones de ecología general, sino que también los convierte en socioecosistemas modelo con los que podemos preguntarnos aspectos de evolución, domesticación, y de la relación entre producción y conservación, entre otras cosas. Se puede investigar cómo las HOI y sus efectos se ven alterados en diferentes esquemas de manejo agrícola, y cómo las redes resultantes de distintos tipos de gestión se integran en los paisajes. Esta perspectiva, en términos de la matriz agrícola, es crucial para fomentar paisajes productivos más sostenibles.

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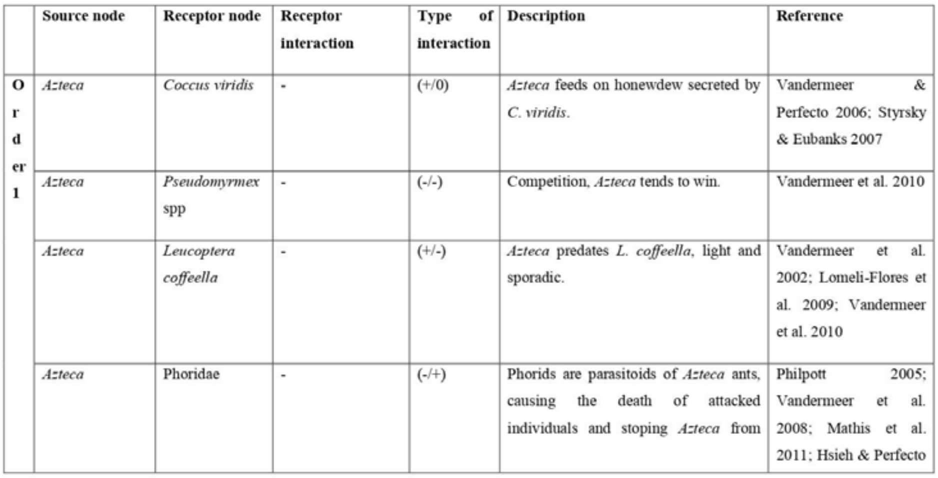
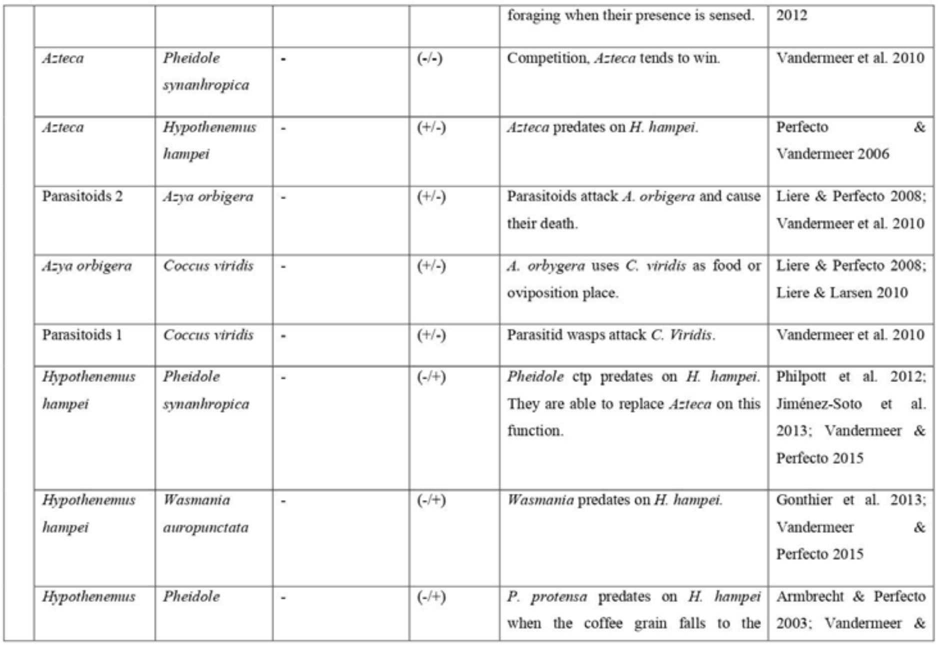
APÉNDICE I: Material suplementario al capítulo II.

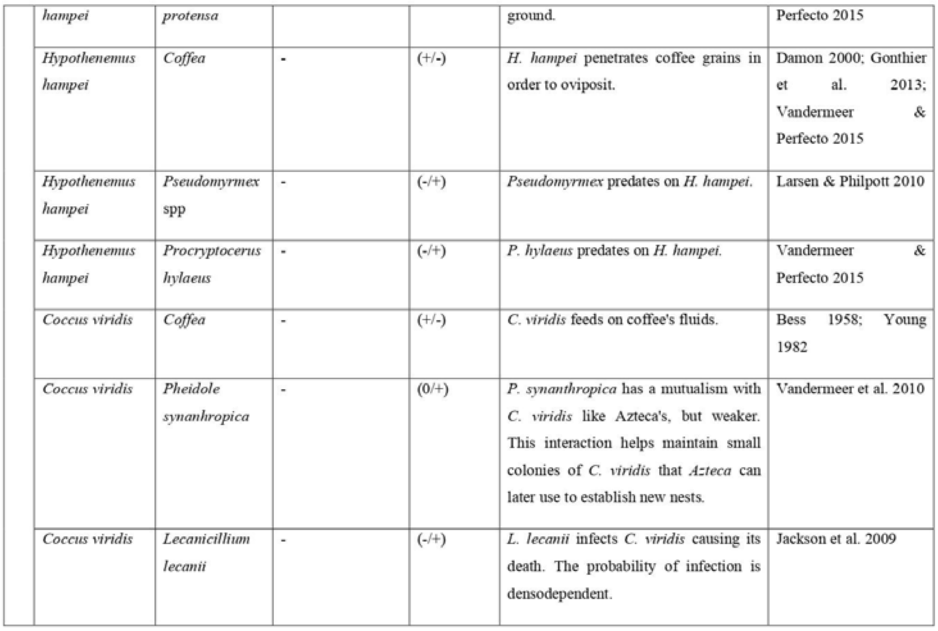
3. **Supplementary Material**

Table S1. Complete database containing all nodes and interactions included in the network, as well as references supporting them.





	Source node	**Receptor node**	**Receptor interaction**	**Type of interaction**	**Description**	**Reference**
Order 1	*Azteca*	*Coccus viridis*	-	(+/0)	*Azteca* feeds on honewdew secreted by *C. viridis*.	Vandermeer & Perfecto 2006; Styrsky & Eubanks 2007
	Azteca	*Pseudomyrmex* spp	-	(-/-)	Competition, *Azteca* tends to win.	Vandermeer et al. 2010
	Azteca	*Leucoptera coffeella*	-	(+/-)	*Azteca* predates *L. coffeella*, light and sporadic.	Vandermeer et al. 2002; Lomeli-Flores et al. 2009; Vandermeer et al. 2010
	Azteca	Phoridae	-	(-/+)	Phorids are parasitoids of *Azteca* ants, causing the death of attacked individuals and stoping *Azteca* from foraging when their presence is sensed.	Philpott 2005; Vandermeer et al. 2008; Mathis et al. 2011; Hsieh & Perfecto 2012
	Azteca	*Pheidole synanhropica*	-	(-/-)	Competition, *Azteca* tends to win.	Vandermeer et al. 2010
	Azteca	*Hypothenemus hampei*	-	(+/-)	*Azteca* predates on *H. hampei*.	Perfecto & Vandermeer 2006
	Parasitoids 2	*Azya orbigera*	-	(+/-)	Parasitoids attack *A. orbigera* and cause their death.	Liere & Perfecto 2008; Vandermeer et al. 2010
	Azya orbigera	*Coccus viridis*	-	(+/-)	*A. orbygera* uses *C. viridis* as food or oviposition place.	Liere & Perfecto 2008; Liere & Larsen 2010
	Parasitoids 1	*Coccus viridis*	-	(+/-)	Parasitid wasps attack *C. Viridis*.	Vandermeer et al. 2010
	Hypothenemus hampei	*Pheidole synanhropica*	-	(-/+)	*Pheidole* ctp predates on *H. hampei*. They are able to replace *Azteca* on this function.	Philpott et al. 2012; Jiménez-Soto et al. 2013; Vandermeer & Perfecto 2015
	Hypothenemus hampei	*Wasmania auropunctata*	-	(-/+)	*Wasmania* predates on *H. hampei*.	Gonthier et al. 2013; Vandermeer & Perfecto 2015
	Hypothenemus	*Pheidole*	-	(-/+)	*P. protensa* predates on *H. hampei* when the coffee grain falls to the	Armbrecht & Perfecto 2003; Vandermeer &



	hampei	*protensa*			ground.	Perfecto 2015
	Hypothenemus hampei	*Coffea*	-	(+/-)	*H. hampei* penetrates coffee grains in order to oviposit.	Damon 2000; Gonthier et al. 2013; Vandermeer & Perfecto 2015
	Hypothenemus hampei	*Pseudomyrmex* spp	-	(-/+)	*Pseudomyrmex* predates on *H. hampei*.	Larsen & Philpott 2010
	Hypothenemus hampei	*Procryptocerus hylaeus*	-	(-/+)	*P. hylaeus* predates on *H. hampei.*	Vandermeer & Perfecto 2015
	Coccus viridis	*Coffea*	-	(+/-)	*C. viridis* feeds on coffee's fluids.	Bess 1958; Young 1982
	Coccus viridis	*Pheidole synanhropica*	-	(0/+)	*P. synanthropica* has a mutualism with *C. viridis* like Azteca's, but weaker. This interaction helps maintain small colonies of *C. viridis* that *Azteca* can later use to establish new nests.	Vandermeer et al. 2010
	Coccus viridis	*Lecanicillium lecanii*	-	(-/+)	*L. lecanii* infects *C. viridis* causing its death. The probability of infection is densodependent.	Jackson et al. 2009

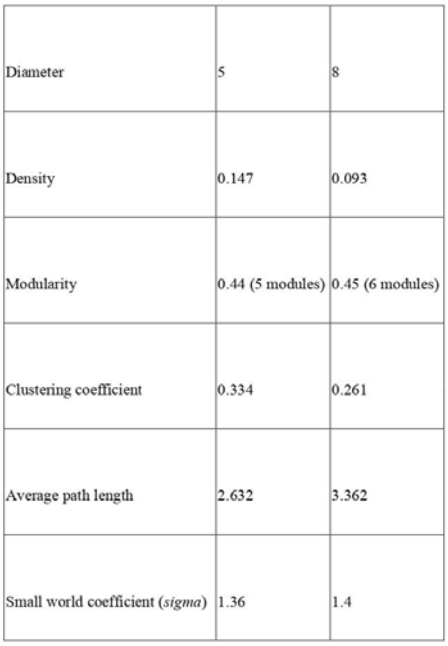
	Hemileia vastatrix	*Lecanicillium lecanii*	-	(-/+)	*L. lecanii* infects *H. vastatrix*.	Vandermeer et al. 2009
	Hemileia vastatrix	*Coffea*	-	(+/-)	*H. vastatrix* infects coffee.	Avelino et al. 2004
	Birds and bats	Herbivores	-	(+/-)	Birds and bats predate on herbivores.	Perfecto et al. 2004; Kalka et al. 2008; Williams-Guillén et al. 2008; Johnson et al. 2010; Mooney et al. 2010
	Birds and bats	Spiders	-	(+/-)	Birds and bats predate on spiders.	Philpott et al. 2004; Mooney et al. 2010
	Spiders	Parasitoids 3	-	(+/-)	Spiders predate on parasitoids 3.	Ibarra-Núñez et al. 2001; Schoener et al. 2002
	Parasitoids 3	Herbivores	-	(+/-)	Parasitoids 3 attack multiple herbivores.	Ibarra-Núñez et al. 2001; Schoener et al. 2002; Vandermeer & Perfecto 2015
	Spiders	Herbivores	-	(+/-)	Spiders predate on multiple herbivores.	Hodge 1999; Schmitz & Sokol-Hessner 2002
	Herbivores	*Coffea*	-	(+/-)	Multiple herbivores predate on coffee.	Vandermeer & Perfecto 2015
	Pheidole synanthropica	*Pheidole protensa*	-	(-/-)	Competition. *P. protensa* tends to win.	Vandermeer et al. 2010
	Pheidole synanthropica	*Pseudomyrmex* spp	-	(-/-)	Competition. *Pheidole* tends to win.	Vandermeer et al. 2010
	Native bees	*Coffea*	-	(+/+)	Native bee diversity promotes pollination and heavier coffee grains.	Kremen et al. 2002; Klein et al. 2003; Klein et al. 2007
	Apis mielifera	Native bees	-	(-/-)	*Apis mielifera* competes with native bees and dominates when there is a low diversity of native shrubs and trees.	Jha & Vandermeer 2009
	Leucoptera coffeella	*Coffea*	-	(+/-)	*L. coffeella* oviposits on coffee leaves, harming coffee.	Fragoso et al. 2002; Lomeli-Flores et al. 2009
	Coccus viridis	*Pseudomyrmex* spp	-	(-/+)	Pseudomyrmex predates on *C. viridis*	Vandermeer et al. 2010

	Leucoptera coffeella	*Pseudomyrmex* spp	-	(-/+)	*Pseudomyrmex* spp predates on *L. coffeella*	De la Mora et al. 2008
	Birds and bats	*Hypothenemus hampei*	-	(+/-)	Birds and bats predate on *H. hampei*	Johnson et al. 2010
Order 2	*Azteca*	-	*Azya*'s oviposition under *C. viridis* or *Azya*'s predation of *C. viridis*.	inhibition	*Azteca*'s protection stops *Azya* from predating on or ovipositing under *C. viridis*.	Vandermeer & Perfecto 2006; Liere & Larsen 2010; Vandermeer et al. 2010
	Azteca	-	Parasitoidism 2 of *Azya*.	inhibition	*Azteca*'s foraging on coffee plants scares off parasitoids that would otherwise attack *Azya* orbigera.	Liere & Perfecto 2008; Vandermeer et al. 2010
	Azteca	-	Parasitoidism 1 of *C. viridis*.	inhibition	*Azteca*'s protection stops parasitoid wasps from attacking *C. viridis*.	Vandermeer & Perfecto 2006; Vandermeer et al. 2010
	Azteca	-	General herbivory of coffee from multiple organisms.	inhibition	*Azteca*'s foraging on coffee plants scares off multiple herbivores.	Styrsky & Eubanks 2007; Vandermeer & Perfecto 2015
	Azteca	-	*H. hampei*'s penetration of coffee grains.	inhibition	*Azteca* grabs *H. hampei* and throws it off the coffee plants, generally without harming it.	Jiménez-Soto et al. 2013
	Phoridae	-	Mutualism between *Azteca* and *C. viridis*	inhibition	The presence of phorids paralizes *Azteca*, stoping them from foraging on *C. viridis* honeydew.	Pardee & Philpott 2011
	Phoridae	-	Interaction between *Azteca* and *L. coffeella*.	inhibition	The presence of phorids paralizes *Azteca*, stoping them from predating on *L. coffeella*.	Vandermeer & Perfecto 2015
	Pheidole synanthropica	-	*Azya*'s oviposition under *C. viridis* or *Azya*'s predation of *C. viridis*.	inhibition	*P. synanthropica* has a mutualism with *C. viridis* like *Azteca*'s, but weaker. This interaction helps maintain small colonies of *C. viridis* that *Azteca* can later use to establish new nests.	Vandermeer et al. 2010
	Pheidole synanthropica	-	Parasitoidism 1 of *C. viridis*.	inhibition	P. synanhropica has a mutualism with *C. viridis* like *Azteca*'s, but weaker. This interaction helps maintain small colonies of *C. viridis* that *Azteca* can later use to establish new nests.	Vandermeer et al. 2010
Ord	Phoridae	-	*Azteca*'s inhibition of parasitoidism 1 of *C. viridis*. (2nd	inhibition	The presence of phorids paralizes *Azteca*, stoping them from inhibiting wasp parasitoidsm of *C. viridis*.	Vandermeer & Perfecto 2015

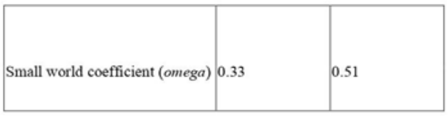
er **3**			order interaction).			
	Phoridae	-	*Azteca*'s inhibition of coffee herbivory from multiple organisms. (2nd order interaction).	inhibition	The presence of phorids paralizes *Azteca*, stoping them from inhibiting herbivory of multiple organisms on coffee.	Vandermeer & Perfecto 2015
	Phoridae	-	*Azteca*'s inhibition of *H. hampei*'s penetration of coffee grains. (2nd order interaction).	inhibition	The presence of phorids paralizes *Azteca*, stoping them from throwing *H. hampei* off coffee plants. Ants like *P. symplex* and *P. hylaeus* are able to replace this function.	Pardee & Philpott 2011; Philpott et al. 2012
	Phoridae	-	*Azteca*'s inhibition of interaction between *Azya* and *C. viridis*. (2nd order interaction).	inhibition	The presence of phorids paralizes *Azteca*, stoping them from protecting *C. viridis* from *A. orbigera*.	Hsieh et al. 2012
	Phoridae	-	*Azteca*'s inhibition of parasitoidism 2 of *Azya orbigera*. (2nd order interaction).	inhibition	The presence of phorids paralizes *Azteca*, stoping them from scaring off parasitoids of *A. orbigera*.	Vandermeer & Perfecto 2015

Table S2. General metrics obtained for the network with and without HOIs: number of nodes, number of edges, mean degree, diameter, density, modularity (using the Louvain algorithm), clustering coefficient, mean path length, and *sigma* and *omega* small world coefficients (Humphries & Gurney 2008; Telesford et al. 2011).

	Without HOIs	*With HOIs*
Nodes	22	34
Edges	68	104
Average degree	3.091	3.059



Diameter	5	8
Density	0.147	0.093
Modularity	0.44 (5 modules)	0.45 (6 modules)
Clustering coefficient	0.334	0.261
Average path length	2.632	3.362
Small world coefficient (*sigma*)	1.36	1.4



Small world coefficient (*omega*)	0.33	0.51

Table S3. ANOVA analyses for the robustness of all networks.

		Degrees of freedom	Sum of squares	Mean sum of squares	Statistic	*p* value	*eta* square	*omega* square	*epsilon* square
Random node removal	Empirical with HOIs vs without HOIs	1	0.019	0.019	0	0.994	0	-0.003	0
	Random with HOIS vs without HOIs	1	0.014	0.014	0.17	0.68	0	-0.002	-0.002
	Small-world with HOIs vs without HOIs	1	1774.66	1774.66	72.14	<0.001	0.153	0.151	0.426
	Scale-free with HOIs vs without HOIs	1	50986.63	50986.63	4463.04	<0.001	0.918	0.918	3.349
By degree node removal	Empirical with HOIs vs without HOIs	1	4721.893	4721.893	495.621	< .001	0.555	0.553	0.554
	Random with HOIS vs without HOIs	1	34281.86	34281.86	236.54	<0.001	0.373	0.371	0.771
	Small-world with HOIs vs without HOIs	1	9312.47	9312.47	333.91	<0.001	0.456	0.454	0.916
	Scale-free with HOIs vs without HOIs	1	50922.49	50922.49	964.08	<0.001	0.708	0.707	21022.325

APÉNDICE II: Material suplementario al capítulo III.

Supplementary material

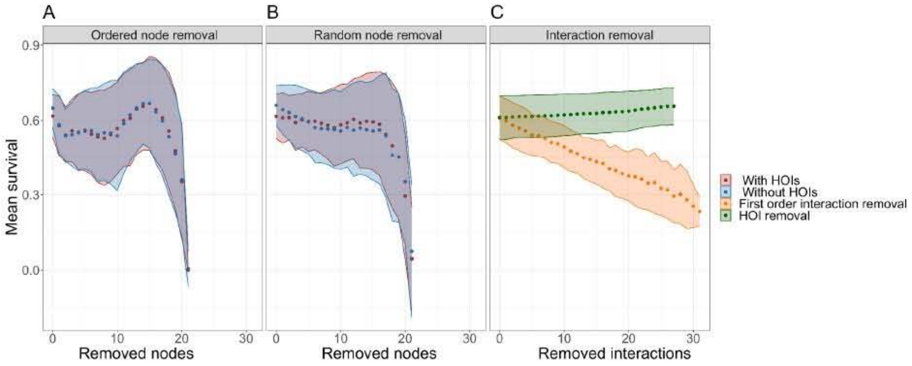


Figure S. 1. A: Mean species survival (where 1 means that all species in the community survived and 0 means none did) as nodes are removed one-by-one in a descending order of node degree. B: Mean species survival as nodes are randomly removed one-by-one. C: Mean species survival as interactions are randomly removed one-by-one. In A and B, red dots represent simulations performed in networks where HOIs are included and blue dots represent simulations where HOIs are not included. In C, orange dots represent networks where first order interactions were removed and green dots represent networks where HOIs were removed. Vertical lines are standard deviations and λ=0.5.

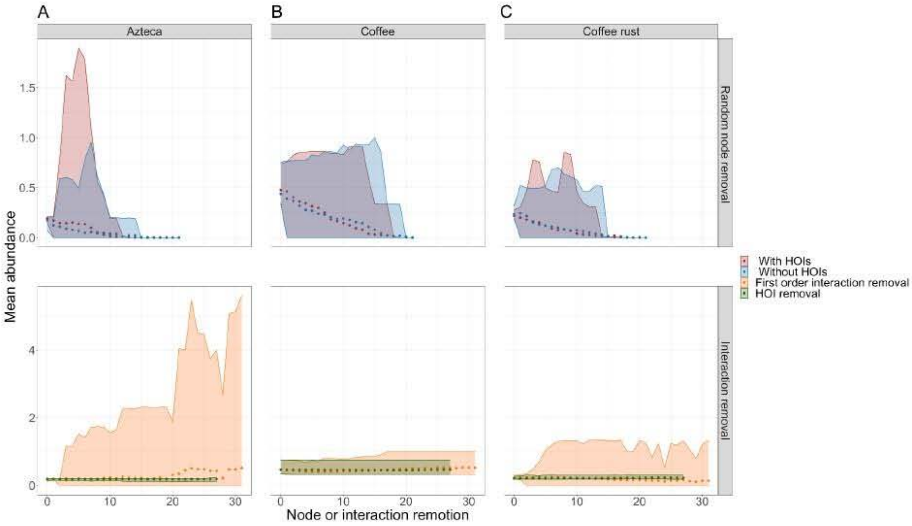


Figure S. 2. A: Mean abundance of *Azteca* ant as nodes are randomly removed (top) and as interactions (bottom) are randomly removed one-by-one. B: Mean abundance of Coffee as nodes are randomly removed (top) and as interactions (bottom) are randomly removed one-by-one. C: Mean abundance of Coffee Rust as nodes are randomly removed (top) and as interactions (bottom) are randomly removed one-by-one. In the top graphs, red dots represent simulations performed in networks where HOIs are included and blue dots represent simulations where HOIs are not included. In the bottom graphs, orange dots represent networks where first order interactions were removed and green dots represent networks where HOIs were removed. Colored shadows represent confidence intervals (prob=0.025) and λ=0.5.

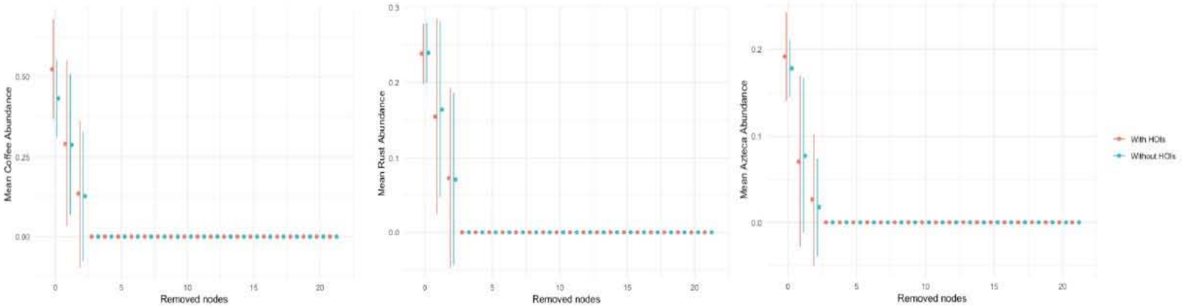


Figure S. 3. Abundance of coffee, coffee rust and *Azteca* ant under ordered-by-degree node removal. The three species have a high degree and hence get removed too soon in the simulations. Red dots represent simulations performed in networks where HOIs are included and blue dots represent simulations where HOIs are not included. λ=0.05.

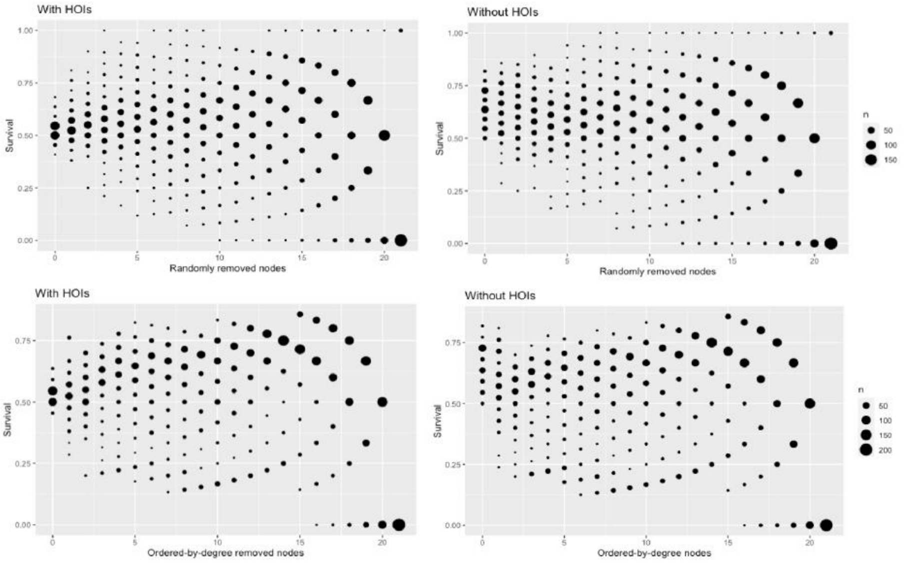
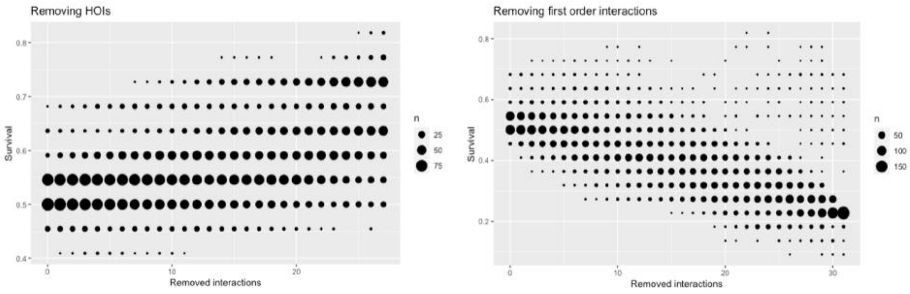


Figure S. 4. Survival in communities as nodes were randomly removed in the network with HOIs (left) and in the network without HOIs (right). At the top we can see simulations where nodes were removed randomly and at the bottom, simulations where nodes were removed by descending order-of-degree. Dot size indicates the number of simulations that reached each value of survival. λ=0.05.



APÉNDICE III: Dispersal and time arrangement condition the timing and magnitude of coffee rust infection

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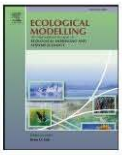

Dispersal and plant arrangement condition the timing and magnitude of coffee rust infection

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ABSTRACT

One central issue in coffee-leaf rust (*Hemileia vastatrix*) epidemiology is to understand what determines the intensity and the timing of yearly infections in coffee plantations. However, most experimental and theoretical studies report infection as an average at the plot level, obscuring the role of potentially key factors like rust dispersal or the planting pattern. Here, we first review the rust epidemic patterns of different sites, which reveal large variability in the duration and magnitude of the different epidemiologic phases. We then present a spatially explicit and parametrised model, where the host population is subdivided into discrete patches linked through spore dispersal, modeled as simple diffusion. With this model, we study the role of the planting arrangement, the dispersal intensity and plant-level variables on the maximum average tree infection (MATI) and its timing. Our results suggest that the epidemic timeline can be divided into two phases: a time lag and a growth phase *per se*. The model shows that the combination of the dispersal magnitude and plant aggregation modifies the MATI and the time to MATI, mainly by preventing some plants from reaching their maximum peak during the epidemic. It also affects the epidemic curves, which can have a stepped, or a rather smooth pattern in plots with otherwise similar conditions. The initial rust infection modulates the time lag before the epidemic and the infected leaf-fall rate drastically changes the MATI. These findings highlight the importance of explicitly considering the spatial aspects of coffee agroecosystems when measuring and managing rust infection, and help us to further understand the spatio-temporal dynamics of ecological systems in general.

1. Introduction

The first recorded epidemic of the coffee rust disease, caused by the fungus *Hemileia vastatrix,* broke out in Ceylon (now Sri Lanka) in 1869 (Talhinhas et al., 2017). Since then, coffee rust has spread across the continents, reaching virtually all the coffee plantations areas on earth (Avelino et al., 2006; McCook and Vandermeer, 2015). This is particularly relevant for farmers who depend economically on these crops.

One central issue in coffee rust epidemiology is to understand what determines the intensity of a one-year infection (Avelino et al., 2006; Gagliardi et al., 2020; Kushalappa and Eskes, 1989; Motisi et al., 2022). Similarly, many epidemiologists have sought to estimate the time to maximum infection for the design of specific control practices (Ananth, 1969; Burdekin, 1964). Both questions have been studied within the "disease triangle" framework (Stevens, 1960). In this sense, scientists and farmers have studied the pathogen's properties such as its genetics (Carvalho et al., 2011), the host resistance and phenology (Avelino et al., 1993; Silva et al., 2006), and disease environmental drivers such as the temperature, humidity or precipitation (Avelino et al., 2015). Nevertheless, there is a large amount of variability in the intensity and timing of the different epidemiological phases of the coffee rust epidemic that remains unexplained, even between neighbouring coffee plots with the same environmental and biotic conditions (Li et al., 2022). For example, in some plantations, when the abiotic and biotic conditions

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for rust invasion are met, the infection may not start right away: there is a highly variable time lag (Boudrot et al., 2016; Mulinge and Griffiths, 1974).

To explain this variability, previous research has mainly focused on the infection phase *per se* (where susceptible leaves are infected by coffee rust spores and become infective; Talhinhas et al., 2017) and has overlooked another epidemiological phase: dispersal. Dispersal is the process by which spores are transported from one place to another, across different scales, ranging from the intraleaf, interleaf, or even the interplot scale (Becker and Kranz, 1977; Boudrot et al., 2016; Vandermeer et al., 2018). Overall, the intensity of an epidemic is highly related to the rates of infection and dispersal during each season (Avelino et al., 2015). Analysis of dispersal is thus called for, and, by its very nature, must incorporate a spatial approach (Avelino et al., 2012). There are effectively two distinct scales of dispersal: first, the large scale mediated by the wind and resulting from a "rain" of spores over large areas (between plots or between farms; Becker and Kranz, 1977; Bowden et al., 1971; Kushalappa and Eskes, 1989), and second, the local scale, corresponding to neighbouring plants in a plot and/or leaves on the same plant, caused mainly by insect vectors, splash, wind gusts, and human action during harvest (Becker and Kranz, 1977; Vandermeer et al., 2018). In this work, we will focus on the local plant-to-plant dispersal scale in a plot.

Intuitively higher local dispersal should lead to more severe epidemics in a plot. However, despite the importance of a nuanced understanding of rust epidemic dynamics within plots, most empirical studies on coffee rust epidemics report rust prevalence in terms of averages within a plot and not on individual trees (Bock, 1962a; Burdekin, 1964). This method reduces the sampling errors and smooths the epidemic curves but may obscure the relationship between plant and plot dynamics mediated by dispersal. Besides, coffee plantations can be arranged in rows or follow a more random arrangement depending on the age, type (rustic or conventional), or size of the plantation (Hajian-Forooshani and Vandermeer, 2021; Moguel and Toledo, 1999). Therefore coffee rust dispersal effect might be modulated by these planting patterns (Hajian-Forooshani and Vandermeer, 2021; Vandermeer et al., 2018). Finally, the relative importance of the dispersal between plants and the plant-level infection dynamics (such as the initial infection or the rust-infected leaf-fall rate) on the plot-level rust epidemics, has not been fully assessed or considered in current dynamic models (but see Park et al., 2001).

A dynamical modeling approach at both the plant and plot scales can help to disentangle such multi-scaled relations and processes, and shed light on the role of dispersal on the maximum infection prevalence (we will refer here to maximum infection) and the time to reach it in coffee plantations. We hypothesise that spatial dynamics and coffee rust dispersal might also play a role in the variability of the timing and magnitude of the different rust epidemiological phases in coffee plots with otherwise similar biotic and abiotic conditions. We thus seek to explore the determinants of (a) the plot-averaged maximum infection and (b) its timing, using a parametrised epidemiological SIX (Susceptible-Infected-eXternal inoculum) model in a spatially structured host population. With this model we analyze the role of the intensity of rust dispersal, planting arrangements, initial infection, and plant-level dynamics (such as the fall rate of an infected leaf) on the epidemiological outcomes.

2. Methods

We first reviewed quantitative and qualitative data on the maximum infection and the number of days to reach this maximum in different coffee systems. From these data, we estimated the duration of the different coffee rust epidemiological phases and their variability, and used them for future validation of the model. Secondly, we built a spatially explicit model to study the role of planting arrangement, dispersal intensity, plant-level dynamics, and initial conditions on the variability detected in the spatially-averaged maximum coffee rust infection and its timing. Details are presented below, but the overall work route was the following: We first constructed the model and parametrised it. Then, we implemented different computational scenarios at the plant and plot level, and studied their effect on the maximum infection, growth phase and time lags.

2.1. Reviewing the qualitative dynamics of coffee rust infection

To study the qualitative behavior of coffee rust infections, we reviewed literature reporting data on coffee rust at coffee sites with different climatic, orographic, and management conditions. We used data from studies that presented at least a 12 month time series, rainfall pattern, and, in some cases, the harvesting period. We explored publications reporting all these data from the 1960′s to the present. Since most of the reviewed works do not report Tables or do not follow a uniform procedure, we extracted both the rainfall and coffee rust infection data directly from the graphs, using WebPlotDigitizer (Drevon et al., 2017; Rohatgi, 2020). We transformed all dates to their corresponding julian day number and all the precipitation histograms to millimetres. Some graphs started on day 250 (September 7th) and others on day 1 (January 1st) (Fig. 2). We considered three time series from Chiapas, México (Avelino et al., 1991; Vandermeer et al., 2018); two from Central America (Quetzaltenango, Guatemala and Turrialaba, Costa Rica) (Avelino et al., 1993; Boudrot et al., 2016); one from South India (Mysore) (Ananth, 1969); and three from Kenya (East Riff, Ruiru and Kiambu) (Becker and Kranz, 1977; Bock, 1962a; Mulinge and Griffiths, 1974). In the case of Ruiru, Kenya, rainfall was not directly reported, so we used the rainfall pattern reported for Nairobi, which has similar climatic conditions (Ndolo et al., 2017).

In some cases, coffee rust infection was reported as the average percentage of rust-infected leaves per tree, in others, as spores counted per tree or spores in the immediate vicinity. Rainfall was reported on a daily or monthly basis, and we grouped the daily data in months. When the harvesting period was reported, we added it manually, adding a ten day-error to each end. For each site, we reviewed the duration of the different epidemiological phases, the maximum infection reached and their relationship with rainfall and harvesting period. We defined the beginning of the rainy season as the middle of the first month that averaged precipitations higher than 50 mm, and the beginning of the epidemic growth period *per se* as the moment when the increase in the reported percentage of infected leaves in the trees was higher than 0.1 per day. The time between these two points was defined as the time lag. Other characteristics of the plantations such as the climatic, orographic, and management conditions are included in the supplementary material S2. The general timings and magnitudes of infection on these sites were also compared to the predictions of our parametrised model.

2.2. SIX model construction

We modeled the dynamics of multiple individual plants, including both infection and internal leaf-to-leaf spore dispersal processes, coupled in a plot through a plant-to-plant dispersal mechanism. The overall modeling strategy is shown in Fig. 1 and can be summarised as follows. We first defined a 10×10 lattice (100 cells) with sink boundaries and 50 trees (N) in four different scenarios of planting arrangements: aggregated, random, rows, and spaced (Fig. 1B). These arrangements aim to represent the different patterns reported in coffee plots, where trees can be closely surrounded by other trees (aggregated), or have direct neighbours in one specific direction (rows), or have no direct neighbours (spaced) or have a random arrangement. Black squares represent the trees with susceptible or infected leaves as well as the immediate space around the tree where external uredospores may be present. White squares represent regions of space where only uredospores might be present ($S = I = 0$ in Eq. (2.2)) (Fig. 1B). We characterised the four different planting arrangements with a distance-between-plant index $\langle H \rangle$ defined as (Eq. (2.1)):

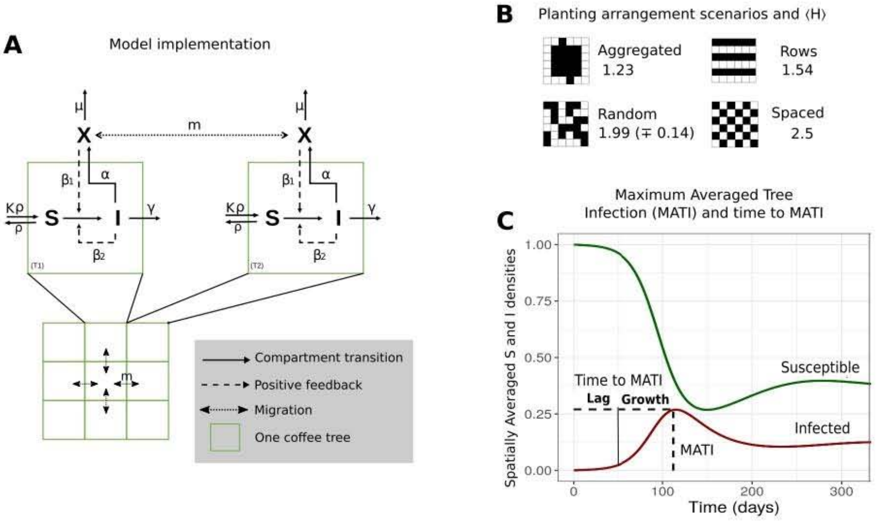

Fig. 1. Model Diagram and the different planting patterns considered. A. Model scheme; S: Susceptible leaves, I: Infected Leaves, X: External spores. B. Different planting arrangements and their distance-between-plants index $\langle H\rangle$. The black squares indicate the presence of a tree and the number is the $\langle H\rangle$ value for that pattern. All the arrangements contain 50 trees in a 10 × 10 lattice (here we depict a 6 × 6 lattice with the same planting density only for visualisation purposes). C. Basic dynamics for S and I, Maximum Average Tree Infection (MATI) and time to MATI (divided in two parts: the time lag (*Lag*) and the growth *per se* (*Growth*)). X follows dynamics similar to I (see Fig. S1.1). Here $\gamma = 0.056$, $\alpha = 0.65$, $\beta_1 = \beta_2 = 0.035$, $\rho = 0.011$ and $\mu = 0.2$ (estimated parameters shown in Table 1).

$$\langle H\rangle = \frac{N}{\sum_{i=1}^{N} H_i} \qquad H_i = \frac{\sum_{j=1}^{4} 1\Big/ d_{ji}}{4} \tag{2.1}$$

where N is the number of plants per plot, and H_i is the average of the inverse distance (number of squares) between plant i and its four closest neighbours j (d_{ji}) along the horizontal and vertical axis. If there are no neighbours along a particular direction, we set $1/d_{ji} = 0$. In the case of the random arrangement, we ran 30 configurations and presented the average. Since we chose the same number of trees for all the scenarios ($N = 50$), $\langle H\rangle$ only depends on the spatial arrangement of plants (Fig. 1B).

Each tree follows the two main phases of the coffee rust life cycle: host-pathogen interaction (invasion) and pathogen dispersal, whose dynamics are schematized in Fig. 1A and are described by the following system of coupled differential equations (Eq. (2.2)):

$$\frac{dS_i}{dt} = \rho(K - S_i) - \beta_1 X_i \frac{S_i}{K} - \beta_2 I_i \frac{S_i}{K}$$

$$\frac{dI_i}{dt} = \beta_1 X_i \frac{S_i}{K} + \beta_2 I_i \frac{S_i}{K} - \gamma I_i \tag{2.2}$$

$$\frac{dX_i}{dt} = \alpha I_i - \mu X_i + m\left(\sum_{j=1}^{V_i} X_{ji} - V_i X_i\right)$$

where S_i and I_i are the amounts of susceptible and infected leaves in tree i. I_i represents the state where the infected leaf has already produced new infective spores. X_i represents the number of infective external uredospores (from now on "external spores"; supplementary material S3; Bock, 1962b) in square i, with or without a tree. X_i does not include spores in the leaves or between them, only the ones that are outside the tree. Host reproduction (*i.e.* leaf production and leaf-fall rate of susceptible leaves) is represented by the so-called monomolecular growth (Cunniffe and Gilligan, 2010), where the natural (or non-infected) leaf-fall rate is represented by ρ and leaf production rate is equivalent to $K\rho$ where K is the carrying capacity of susceptible leaves. We took $K = 1$ for simplicity but our results can be rescaled by using reported values for K (Burdekin, 1964). This assumes that the new leaf production rate equals the leaf-fall rate of susceptible leaves. The transition from S to I is subdivided into primary infection arising from the external spores (X) and secondary infection occurring by transmission from already infected leaves (I). In both cases, the growth in infection is proportional to the fraction of remaining susceptible leaves S/K, and to the rates (β_1, β_2), respectively. Infected leaves can fall and leave the I compartment at a rate γ that must be higher than the non-infected leaf-fall rate (ρ). Spores detach from infected leaves and become suspended in the air or fall on the ground, filling the X compartment at a rate α. External spores die at rate μ both in squares with and without trees (black and white cells in Fig. 1B). Finally, m is the diffusion rate, which represents the rate at which spores are dispersed to the neighbouring squares. Let us denote as V_i the number of immediate neighbours of square i (ranging from two to four depending on the location of the square in the lattice), and X_{ji} the amount of X in the j-th neighbour of i. Non-directed dispersal is modeled by a diffusion process that takes place from one plant to its four immediate neighbouring squares, mimicking short ranged rust dispersal mediated by splash and plant-to-plant contact in our two-directional planting arrangements. Note that equivalent scenarios could be modeled using an 8 neighbourhood vicinity, but in order to create the spaced arrangement we would have to push trees further away from each other. In empty squares, $S_i = I_i = 0$, so the spores have the following dynamic:

$$\frac{dX_i}{dt} = m\left(\sum_{j=1}^{V_i} X_{ji} - V_i X_i\right).$$

All the parameters are summarised in Table 1.

Our model is a spatially extended case of the SIRX (Susceptible-Infected-Removed-eXternal inoculum) models analyzed by Cunniffe and Gilligan (2010) and Gubbins et al. (2000), originally developed for insect-pathogen interactions but widely used for plant-pathogen associations (Swinton and Anderson, 1995). Here we did not include the Removed compartment (R) since its dynamic is determined by the other compartments and does not impact the whole infection process (this assumption is discussed in the Discussion section). In this sense, our model can be referred to as a SIX model. We assume that infection happens in non-resistant coffee trees with "well-mixed leaves", when the conditions for the development of coffee rust are optimal (sufficient susceptible leaves and humidity Nutman et al., 1963). Factors like plant or rust variability are not explicitly considered, nor the change in abiotic conditions. In this work we do not study the equilibrium points but rather some of the most relevant transient dynamics of coffee rust epidemics like the duration of the growth phase or the maximum infection, as well as the probability of rust invasion in each individual plant (but see Cunniffe and Gilligan, 2010 for the linear analysis of the model and the supplementary material S1 for the equilibrium points). The invasion criteria is summarised by the parameter R_0 which is defined as (Eq. (2.3)):

$$R_0 = \frac{\beta_2 + \frac{\beta_1 \alpha}{\mu}}{\gamma} \tag{2.3}$$

If R_0 is less than 1, the single plant system always reaches a-non infective equilibrium. If $R_0 \geq 1$, I and X "invade" and S decreases (see Fig. S1.1 and Cunniffe and Gilligan, 2010 for the main mathematical results on this model).

2.3. Plant level parameterization and simulation conditions

We selected the infected leaf-fall rate (ɣ) as the sole plant-level

Table 1
Estimated parameter ranges, definition, estimation methods and used values for SIX model simulations.

Parameter	Definition	Inverse of the time it takes:	Estimation Method	Explanation of the estimation	Units	Range	Used values for simulations
Estimated parameters							
ρ	Natural leaf fall rate	One newly mature susceptible leaf (S) to fall	In field measurement (a) Data-Based Estimation (b, c)	Time reported in the field as GDD (a). We also fitted data of leaf development in trees, where coffee rust infection was negligible, to a basic leaf growth equation (b, c).	1/t	[0.009–0.013]	[0.011]
β1 and β2	Primary and secondary infection rate	One susceptible leaf (S), in contact with one external package of infective spores (X) or with one infected leaf (I), to become infected	In field measurement (d, e)	Time well documented in several field studies (d, e).	$N_{inf}/(N_{sp}$ t) and 1/t	[0.03–0.04]	[0.035]
α	Recruitment rate	One package of spores (X) to leave the plant system from one infected leaf (I)	Data-Based Estimation (f, g, d, h, i)	Estimation based on reports on the number of spores produced per infected leaf and per unit of time, as well as on the relationship between the number of spores in a leaf and the number of spores surrounding the plant system (f, g, d, h, i)	$N_{sp}/(N_{inf}$ t)	[0.1–1.2]	[0.65]
μ	Spore death rate	A new spore to become non-viable.	Data-Based Estimation (j, k)	The spore viability through time has been studied (j, k). We used their data to fit our model.	1/t	[0.1–0.3]	[0.2]
ɣ	Infected leaves fall rate (γ = ρ + ρI)	A newly infected leaf (I) to fall	Data-Based Estimation (c)	Time is shorter than the natural leaf fall time. As far as we know, the former time is not explicitly reported so we used (c) results on susceptible and infected fallen leaves to estimate the leaf fall differences.	1/t	ρ+ [0.004]	[0.015–0.14]
Non-estimated parameters							
K	Carrying capacity of susceptible leaves	NA	NA	NA	N_{leaf}	NA	1
m	Diffusion rate	One package of spores to be fully transported to a 4N-vicinity neighbour square.	NA	NA	1/t	NA	[0.001 – 0.1]

The letters indicate the direct reference used: a- Rakocevic and Takeshi (2018) b- Mulinge and Griffiths (1974), c- Firman and Wallis (1965), D- Bock (1962a), e- Leguizamón-Caycedo et al. (1998), f-Gagliardi et al. (2020), g- Boudrot et al. (2016),h- Rayner (1961), i- Silva-Acuña et al. (1999), j- Nutman et al. (1963), k- Deepak et al. (2012). GDD: Growing Degree Days. N_{sp}: number of infective packages of external spores, N_{leaf}: number of susceptible leaves, N_{inf}: number of infected leaves. NA: Not Applicable.

variable and fixed the other parameters of the SIX equation (primary and secondary infection, recruitment, leaf-growth, and spore-death rates). We chose the infected leaf-fall rate as it is a variable that can be directly modified by human management (e.g. removing and bagging away the infected leaves). The other parameters such as the infection rates are affected by multiple environmental, genetic and management processes and are more difficult to control. Besides, this decision reduces our computational explorations and simplifies the interpretation of the results. To choose the values of the plant-level parameters correctly and work with meaningful timescales, we estimated the range of each plant or spore parameter from reported data (Table 1) (Bock, 1962a; Boudrot et al., 2016; Deepak et al., 2012; Firman and Wallis, 1965; Gagliardi et al., 2020; Leguizamón-Caycedo et al., 1998; Mulinge and Griffiths, 1974; Nutman et al., 1963; Rakocevic and Takeshi Matsunaga, 2018; Rayner, 1961; Silva-Acuña et al., 1999). We then set each parameter to the mean value for our general simulations, but we included a sensitivity analysis of our results, using the lowest and highest values of the estimated ranges. The infected leaf-fall rate (γ) was varied above its estimated mean to account for leaf-removal practices that shorten the time for a rusted leaf to fall (e.g. selective pruning), but we restricted its maximum value to simulate scenarios where rust invades the system (this is, where $R_0 \geq 1$ considering the other estimated parameters; Eq. (2.3)) . The detailed methods for the estimation of each parameter are available in the supplementary material S3. To summarise, the model parameters can be estimated from the characteristic time-scale (in days) of a given known process. We first looked for studies that reported those times directly or indirectly. If these data were not available, we fitted specific time-series of leaf infection to linear or exponential models (Table 1).

2.4. Simulations and measured variables: MATI and time to MATI

With the chosen parameters, we explored the effect of the leaf-fall rate of infected leaves (γ), the initial proportion of infected leaves per tree (I_0), the planting patterns, and the different plant-to-plant diffusion rates (m) on the maximum averaged tree infection (henceforth; MATI) and the time to reach this maximum (in days) (Fig. 1C). The MATI is obtained by averaging tree infection over all trees in the plot for every time step, and then by identifying its overall maximum. This is a common indicator to measure rust infections in the field. The time to MATI was divided into a time lag and a growth period *per se*, following the same criteria used in real time series (see Section 2.1 and Fig. 1C). The results were then compared with the magnitudes measured in Section 2.1 and analyzed in each combination of scenarios.

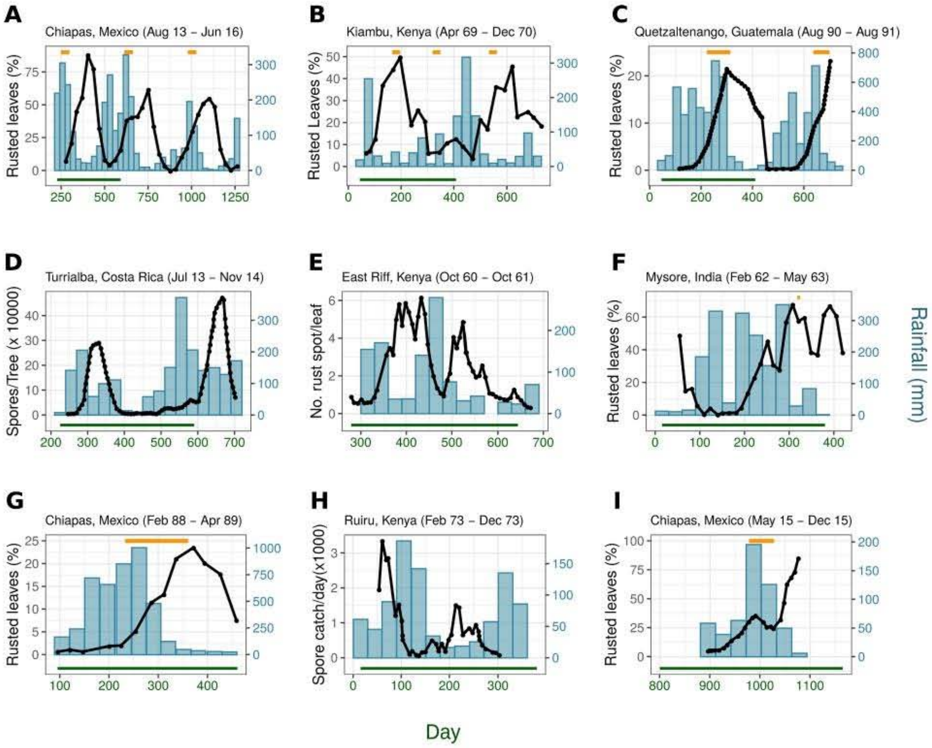

Fig. 2. Coffee rust infection dynamics in relation to annual rainfall and harvesting period. The black line represents the amount of rust infection, measured as the average percentage of rusted leaves per tree (A, B, C, F, G, I), or the average number of rust spots per leaf (E), or the number of spores per tree (D), or above the tree (H). The bars represent the monthly rainfall (mm). The orange horizontal segment in figures A, B, C, F, G and I shows the reported harvesting period and the green horizontal line in the bottom of each graph stands for the 365-day period. The plots are ordered from the longest to the shortest period recorded. The references for each plot are: A (Vandermeer et al., 2018), B (Mulinge and Griffiths, 1974), C (Avelino et al., 1993), D (Boudrot et al., 2016), E (Bock, 1962a), F (Ananth, 1969), G (Avelino et al., 1991), H (Becker and Kranz, 1977; Ndolo et al., 2017), I (Vandermeer et al., 2018). For more details, see supplementary material 2.

2.4.1. One-plant level simulations

We first ran simulations of the SIX model at the single-tree level ($N = 1$, $m = 0$ and $i = 1$), studying the effect of both the γ and I_0 on the MATI and the time to MATI. In this scenario, the MATI is the maximum local tree infection. We varied the leaf-fall rate of infected leaves (γ) from 0.015 to 0.14 and the initial proportion of infected leaves per tree (I_0) from 0.001 to 0.1 (72 scenarios in total). Each simulation started with I_0 infected leaves ($I = I_0$), $1 - I_0$ susceptible leaves ($S = 1 - I_0$), no external uredospores ($X = 0$) and ran for 30 000 integration steps using the Euler method ($\Delta t = 0.01$). This method is a standard and common integration procedure for solving discretized partial differential equations in lattices (Koch and Meinhardt, 1994; Elder et al., 1992) and is sufficiently robust and precise for all our modeled scenarios and quantities of interest (with a $\Delta t = 0.02$, there were no differences in the results within the range of precision used (Fig. S1.6)). These integration steps represented 300 days, after parameter calibration. The beginning of the simulation corresponds to the start of the optimal conditions for infection (when humidity is sufficient, and leaves are susceptible) and we chose 300 days to be the maximum time for the rust to reach the maximum peak of infection in one year (following the times reported in Fig. 2). After this, rust infection is assumed to decrease. This time limit sets a maximum simulation time.

2.4.2. Plot-level simulations

The next step was to run the full model in the 10 × 10 lattice to include the effects of spatial arrangement and diffusion rate on the MATI and time to MATI. We defined scenarios with the four different planting arrangements (aggregated, spaced, random and rows), one initially infected tree in the centre of the lattice ([x,y] = [5,6]), two values of initially infected leaves ($I_0 = 0.001$ and $I_0 = 0.1$), and five different levels of diffusion rate (m) across three orders of magnitude (ranging from 0.001 to 0.1; or expressed in log for a better visualisation, from −3 to −1). We also chose two of the values of γ used in the single plant dynamic (0.015, 0.056) to compare the plant and plot-level results. For the random planting, we took averages over 30 simulations for each combination of the parameters. For each scenario we obtained the MATI and the time to MATI as a function of the diffusion rate, initial infection and $\langle H \rangle$. We also included the time evolution of the average tree infection with two representative diffusion values ($\log(m) = -3$, $\log(m) = -2$). As we consider $t \leq 300$ days, the results of the scenarios can be divided into two cases: **a.** when an infection peak is attained before the 300 days and **b.** when the optimal conditions for rust cease before the peak is reached (creating a maximum at 300 days). Finally, in order to explore the relationship between individual and average dynamics, we registered the values of each tree's maximum infection and timing and grouped the number of trees that reached a high level of infection (more than 70% of infected leaves) during the same 15-day period. Focusing both on the level of infection of individual trees and their degree of temporal overlapping can shed light on the determinants of the average infection dynamics.

2.4.3. Computational implementation

The model and simulations were implemented in the *Python* 3.7.3 programming language, using the modules *NumPy, SciPy, Pandas, Seaborn* and ran on the LANCIS facilities, at the Ecology Institute of UNAM. The data analyzes and figures were done in *Rstudio* 1.2.1335 using *plyr, dplyr, tidyverse, ggplot2* and *patchwork* libraries and *Inkscape 1.0*. All code and data to reproduce results in the work can be accessed at https://github.com/tenayuco/dispersion_plant_arrangement_coffeerust_infection

3. Results

3.1. Trends in qualitative dynamics coffee rust infection: seasonality and variability in time lags, growth phase and maximum infection

Fig. 2 depicts different coffee rust infection dynamics observed in nine sites, the corresponding rainfall, and, when reported, the harvesting period. Each infection is measured either as the average percentage of rusted leaves per tree or as the average number of spores, during at least one year (green bar at the bottom of each plot). Plotting the time series together enables us to visualise similarities and differences. Firstly, rust infection follows a basic epidemiological cycle consisting of a time lag in relation to the beginning of the rainy season, followed by a growth and a decline phase.

Coffee rust infection also seems to have a rain-forced periodicity: the growth phase always starts after the onset of the rain season (this is clearer for Fig. 2A–C where more than one year is reported). This forced periodicity is related to the first phases of the coffee rust infection cycle, where rain is necessary for spores liberation and invasion. The infection reaches a maximum value and declines when the rain season is ongoing (D, H) or has ended (A, C, F, G). In Kenya, where there are two rainy seasons per year, we observe two peaks of infection (Fig. 2B,E,H). The second peaks are substantially lower than the first peaks in East Riff and Ruiru Sites but they are qualitatively relevant to the general dynamics (B, H), as they show that a new infection process began.

The time lag is 82 days on average (ranging from 24.5 (B) to 146 days (C); see Table S1.1). In sites with two rainy seasons, the lag shortens (Fig. 2B,E,H). In some cases, coffee rust infection is negligible during the lag (Fig. 2C,D,F,G). The growth phase takes 119 days on average, ranging from 68 (I) to 181 days (C) (Table S1.1). It is worth noting that the coffee rust infection cycle takes about 30 days, therefore rust probably undergoes multiple infection cycles during one epidemiological phase, as discussed in Kushalappa and Eskes (1989). The "time to maximum infection" comprises the time lag and the growth phase and ranges from 95 (I) to 325 days (C). The maximum average tree infection ranges in turn from 20 to 80% of infected leaves per tree. Therefore, the timing and intensity of an infection at a given site are largely variable. Interestingly, the harvesting period correlates with the build-up (growth phase) (Fig. 2A,C,G,I) (see the discussion section). All values for the MATI and time to MATI are summarised in Table S1.1.

3.2. Estimation of the parameters of the SIX model in a rust-infected scenario

We estimated the natural (non-infected) leaf-fall time, primary and secondary infection, and spore death rates directly from reported data (supplementary material S3; Table 1). The leaf-fall time of susceptible leaves ($1/\rho$) ranges between 74 and 108 days. β_1 and β_2 can both be interpreted as the inverse of the time taken for one susceptible leaf to become infected, either for being in contact with external spores or with an infected leaf. If we assume that one package of external spores infects one leaf at a time (this is $N_{sp}/N_{inf} = 1$) both times are equal and range from 25 to 30 days ($1/\beta_1$ and $1/\beta_2$). Finally, the uredospore viability goes from 3 to 10 days ($1/\mu$) (Table 1). The time taken for a newly infected leaf to fall ($1/\gamma$) was estimated indirectly as how much shorter this time was in comparison to $1/\rho$. Infected leaves take on average from 35 to 53 days less than susceptible leaves to fall.

We express γ as $\rho + \rho_I$, where ρ_I is the increment in leaf-fall rate due to coffee rust infection. The recruitment rate (α) range is broad [0.1–1.2] since it was estimated indirectly from several studies (Table 1). We use $\rho = 0.011$, hence the mean value of γ is equal to 0.015 (Table 1). Given the values chosen for the other parameters here, the invasion criterion can be expressed as $R_0 = 0.15/\gamma \geq 1$ (see Eq. (2.3) and Fig. S1.1). In this sense, to simulate rust infected scenarios and to account for leaf-removal practices (see Section 2.3), γ was varied between 0.015 to 0.14 ($R_0 \in [1, 10]$).

3.3. In one-plant simulations, γ affects both the MATI and time to MATI, and I_0 affects the time to MATI through the time lag

Fig. 3A,B display the maximum averaged tree infection (MATI) and the days to MATI, for one-tree simulations ($N = 1$), varying the leaf-fall

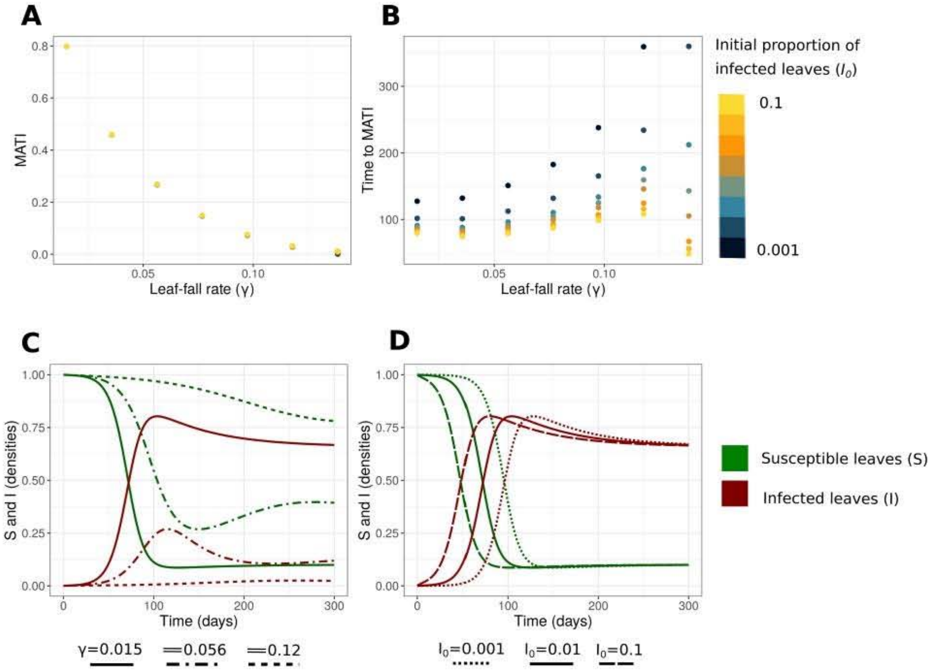

Fig. 3. MATI and time to MATI in isolated coffee plants ($N = 1$). A, B: MATI and days to MATI in function of the leaf-fall rate of infected leaves (γ) and initial proportion of infected Leaves (I_0). C: Example of infection dynamics for susceptible and infected leaves (see Fig. S1.2 for the evolution of the spores X) with different values of γ and a fixed $I_0 = 0.01$. D: Example of infection dynamics with different values of I_0 and a fixed $\gamma = 0.015$. The values of α, β_1, β_2, ρ and μ are shown in Table 1.

rate (γ) and initial proportion of infected leaves (I_0). MATI decreases with the infected leaf-fall rate (Fig. 3A,C). When γ is equal 0.015, the maximum infection is around 75%. When γ is higher than 0.1, MATI drops to zero. This effect is independent of the number of infected leaves in the systems' equilibria predicted by R_0 (Section 2.3; Fig. S1.3; see Fig. S1.1 for the influence of γ on equilibria and stability). I_0 does not affect the MATI whatsoever (Fig. 3D). Time to MATI is affected by both γ (Fig. 3B,C) and I_0 (Fig. 3B,D). In general, when γ increases, the time to reach MATI increases because the curve flattens (Fig. 3C), affecting the growth phase duration but not necessarily the time lag (see Fig. 2). On the other hand, when I_0 is low, the time to MATI increases without changing the MATI (Fig. 3B,D). In other terms, I_0 affects the time lag but not the growth phase *per se* (Fig. 3D). When MATI drops to 0 (with high values of γ) the time to MATI is not relevant since the maximum infection can be reached at the beginning of the simulation.

3.4. In the spatially explicit model, diffusion rate and the planting arrangement jointly modify MATI and days to MATI in a threshold-dependent manner and modify the curves of infection, while I_0 modulates the time lag and γ decreases the MATI in all scenarios

We plotted in Fig. 4 the MATI and time to MATI for each combination of planting arrangement, diffusion, and initial conditions (I_0), and in Fig. 5 the time evolution of the average tree infection with two representative diffusion values ($\log(m) = -3$, $\log(m) = -2$). We used two values of γ (0.015, 0.056) but as the results were qualitatively similar, we only present the plots here for $\gamma = 0.015$ (but see Fig. S1.7 for the case of $\gamma = 0.056$). As we explained in the methods sections, results are divided into two cases: **a.** when an infection peak is attained before the 300 days and **b.** when the optimal conditions for rust cease before the peak is reached (creating a maximum at 300 days).

The variations of the time to MATI and MATI for all the combinations of scenarios fall within the range reviewed in Section 3.1 (see Fig. 2 and Tables S1.1 and S1.2). In all the spatial arrangements, when diffusion rate increases, MATI increases, and days to MATI decrease (Fig. 4).

In the aggregated planting arrangement MATI is always reached before 300 days (ranging from 116 to 287 days) and has values above 70% of infected leaves, only slightly modified by the diffusion rate. In the rows, random and spaced arrangement the change of diffusion rate has a more pronounced effect on the MATI. When the diffusion rate is minimal ($\log(m) = -3$) the time to MATI is 300 days (case b; Figs. 4 and 5). In those scenarios, MATI reaches values that range between 35% and 55% of infected leaves, depending on how advanced the infection was at 300 days. If the diffusion rate is larger (more than −2.5 or −2 depending on the arrangement and the initial infection), the time to MATI becomes less than 300 days for these three arrangements (varying between 151 and 294 days). In these scenarios, an infection peak is reached before the end of optimal conditions (*i.e.* before the end of the simulation; case **a**).

In other terms, for lower values of diffusion rate ($\log(m) = -3$) the change of the diffusion rate affects the MATI according to a critical distance between plants ($\langle H \rangle$): when $\langle H \rangle$ is higher than 1.5, this change greatly modifies the MATI (Figs. 4 and S1.4), when $\langle H \rangle$ is lower than this threshold, the MATI is slightly affected. For higher values of the diffusion rate ($\log(m) > -3$), the differences in aggregation become less relevant. Interestingly, in all scenarios, the diffusion rate modifies the growth time *per se* (that varies between 151 and 205 for $\log(m) = -3$,

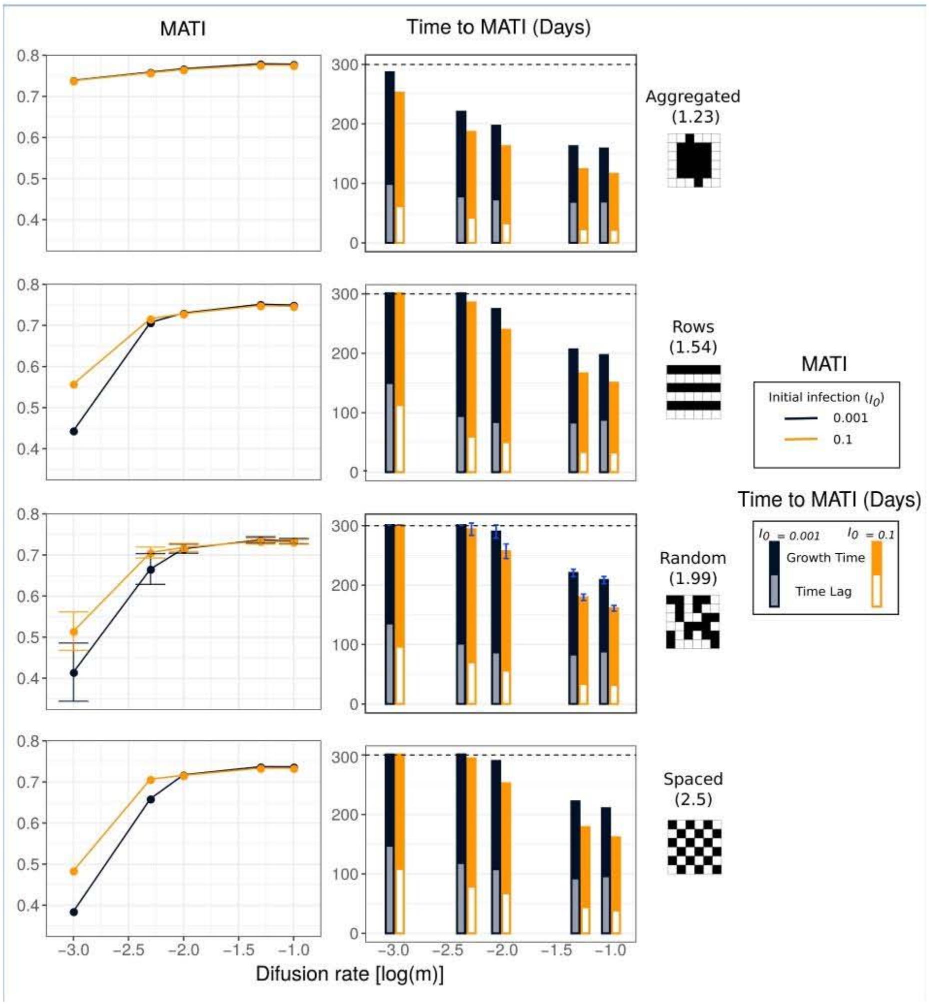

Fig. 4. MATI and time to MATI for all simulations. Simulations of four different planting arrangements (aggregated, random, rows and spaced, with their respective distance-between-plants index ⟨H⟩) with five levels of diffusion rate (log(m) between −3 and −1) and two levels of I_0 (0.001 and 0.1, dark and orange lines, respectively). The bars representing the time to MATI are divided into the time lag and the growth period *per se* (light blue vs black and light orange vs dark orange). The dotted line represents the 300 days limit of the simulations. For the random arrangement, each point/bar represents a 30-simulation average, and the error bars the standard deviation. The values of α, β_1, β_2, ρ and μ are shown in Table 1. We used $\gamma = 0.015$ (see Fig. S1.7 for $\gamma = 0.056$).

and 89 and 129 for log(m) = −1) (see Fig. 4 and Table S1.2). For low diffusion rates, this results in flatter curves leading to lower MATI (Fig. 5).

Moreover, differences in planting arrangements do modify the qualitative average tree infection dynamics, creating smoother or rougher curves (Fig. 5). In particular, the spaced arrangement combined with a low diffusion rate, generates multiple steps in the epidemiological dynamics (Fig. 5). This is similar to what we observe in Fig. 2B or H. Random and row planting arrangements did not present any relevant differences between them.

I_0 mainly affects the time lag (that varies between 70 and 150 days when $I_0 = 0.001$ and between 22 and 113 days when $I_0 = 0.1$) (see Fig. 4 and Table S1.2). The curves of Fig. 5 are thus shifted along the time axis as I_0 varies. It is noteworthy that the time lag can be higher than in the one-plant simulation scenarios (that go from 10 to 50 days as I_0 is varied). This increase in the time lag can lead to a lower MATI if the curve of infection does not reach a maximum peak and is still increasing at the end of the simulation (Figs. 4 and 5).

All of our results were qualitatively robust to the variation of the other plant-level parameters within their estimated range, except for the lowest value of α ($\alpha = 0.1$) that significantly decreases the MATI in all scenarios (Fig. S1.7). Finally, as in the plant-level simulation, the MATI decreases and the time to MATI increases when the infected leaf-fall rate (γ) increases (Fig. S1.7.B), especially for values greater than the

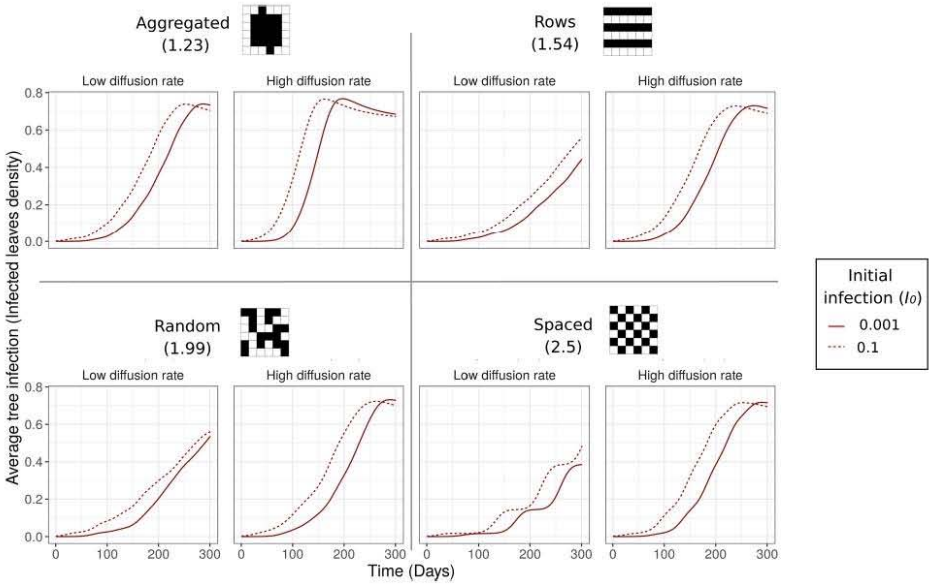

Fig. 5. Examples of average tree infection dynamics for plants in a plot. Simulations of four different planting arrangements (aggregated, random, rows and spaced) with two levels of diffusion (low: $\log(m) = -3$, high: $\log(m) = -2$) and two levels of I_0 (0.001 and 0.1). The lines represent averages over all the trees of the plot at a given time. The values of α, β_1, β_2, ρ and μ are shown in Table 1. We used $\gamma = 0.015$.

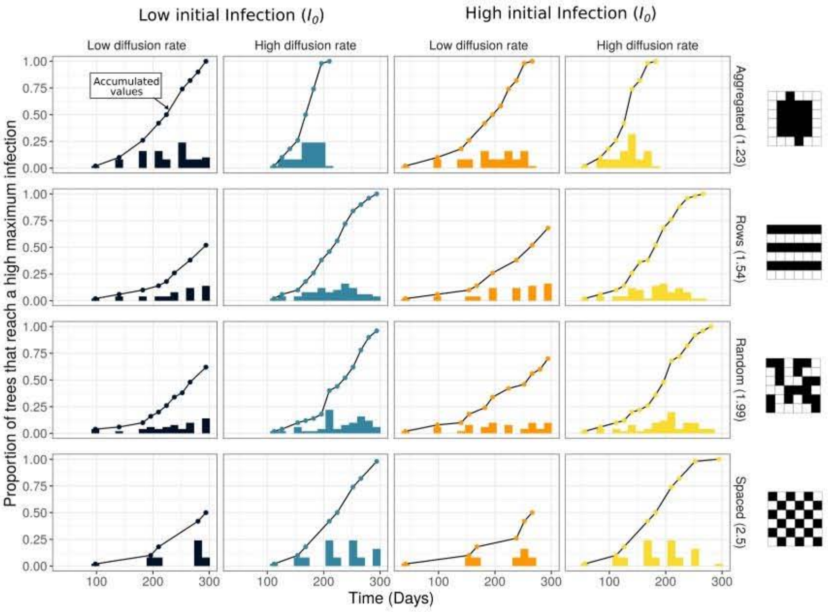

Fig. 6. Proportion of trees that reach a high maximum infection (>0.7 of infected leaves) during the same 15-day period. Histograms for the different planting arrangements (aggregated, random, rows and spaced) with two levels of diffusion (low: $\log(m) = -3$, high: $\log(m) = -2$) and two levels of I_0 (0.001, 0.1; dark/blue and orange/yellow colors, respectively). The black dotted line represents the corresponding accumulated proportion of trees in the plot that reach a high maximum infection. The values of α, β_1, β_2, ρ and μ are shown in Table 1. We used $\gamma = 0.015$.

estimated range ($\gamma = 0.056$).

3.5. The MATI and time to MATI are determined by the number of individual plants that reach a high level of infection before the end of the simulation, and their degree of temporal overlapping

The level of infection of individual trees and their degree of temporal overlapping determine the average infection dynamics. Both variables are affected by the diffusion rate and the planting arrangement. We represent in Fig. 6 the proportion of trees that reached a high level of infection (>70% of infected leaves) during the same 15-day period, and the accumulated proportion of corresponding highly infected trees (dotted line), which indicates how much the epidemic has expanded in space up to a given time (see supplementary material S4 for a full plot visualisation and refer to Fig. S1.5 for the values of each tree's maximum infection and timing).

Planting arrangement substantially influences the overlap between individual tree dynamics. This explains the different shapes of the average infection curves (Fig. 5) as well as the changes in MATI and time to MATI. When plants are spaced, in rows, or randomly distributed, the distribution of the number of highly infected trees over time is broader than in the aggregated pattern, especially when diffusion is high (Fig. 6; yellow and light blue bars). This means that in the first three scenarios the temporal overlap of highly infected trees decreases, which causes a lower MATI compared to the aggregated pattern (Figs. 4 and 6).

The diffusion rate, combined with the planting pattern, affects both the overlap and the individual times at which the maximum individual infection is reached. When diffusion is low (dark blue vs light blue, and orange vs yellow bars in Fig. 6) the distribution is spread out and slightly shifted to the right (see also the accumulated curve). At low diffusion, for the spaced, rows and random patterns, only 50 to 75% of the trees reach the 70% of infected leaves threshold before the end of the simulation. The other trees with low levels of infection will contribute little to the average tree infection value, lowering the MATI (Figs. 4, 5 and S1.5). In the aggregated pattern or when diffusion is high, all the trees reach 70% of infected leaves (the accumulated curves sum up to 1). Interestingly, high values of $\langle H \rangle$ (which characterises rows, random and spaced arrangements) combined with a low diffusion rate (dark and orange bars) generate isolated outbreaks of highly infected trees (Fig. 6). In particular, in the spaced pattern, individual trees reach high infections at well separated times, explaining the multi-stepped dynamics of the spatially averaged prevalence in Fig. 5. Fig. 6 also shows that a lower amount of initially infected leaves (I_0) delays the initial infection without significantly changing the dynamics.

4. Discussion

One of the central issues in coffee rust epidemiology is to understand the factors that explain the great variability in the magnitude of the infection peaks and their timing, both at the plant and plot levels (Avelino et al., 1991; Li et al., 2022; Rosas et al., 2021). To address this issue, many studies have focused on the microclimate (Avelino et al., 2006), plant resistance (Talhinhas et al., 2017), or the susceptibility of leaves during specific stages of the coffee crop cycle (Salgado et al., 2008). Nevertheless, none of these approaches has succeeded to fully explain the differences in timing and intensity of the epidemics occurring in plots from the same site with equivalent meteorological and plant genetic conditions. Here we hypothesised that spatial patterns created by rust dispersal in different planting arrangements might be affecting both variables.

We first documented known trends for the timing and magnitude of the epidemic peak, as well as their variability, by comparing epidemiological curves from different sites (Fig. 2). From this analysis we distinguish two phases in the epidemic timeline: a time lag and a growth phase *per se* (Fig. 2 and Table S1.1). We also noted that the harvesting period correlated with the build-up or growth phase (Fig. 2A,C,G,I). This is consistent with harvesting and rust infection being related to fruit development and fruit load (Avelino et al., 1993; Motisi et al., 2022; Salgado et al., 2008). Nevertheless, the movements of workers during harvesting might also promote rust dispersal and reinforce the infection (Motisi et al., 2022). Our parameterised SIX model recreates the coffee rust epidemic and helps us to explore some of the mechanisms that may determine properties of the maximum peak and its timing (Figs. 3–6). The values of the maximum average tree infection (MATI) and time to MATI were within the range reported in field studies. This qualitatively validates the estimates of the model parameters, and supports that different planting arrangements and different diffusion rates might provide possible explanations to the variation observed in real dynamics.

In particular, we showed that both the planting arrangement and the diffusion rate jointly modify the MATI and time to MATI by preventing some plants from reaching their maximum peak (Figs. 4–6), thus explaining part of the variability observed in plots with otherwise similar conditions. In particular the aggregated spatial arrangement highly increases the MATI compared to the other planting arrangements that did not present quantitative differences between them (see video in supplementary material S4). The effects of the planting arrangement are noticeable in the different curves of Fig. 5, which can be multi-stepped, or smooth (like some of the curves from real data presented in Fig. 2). The multi-stepped pattern is associated with a higher distance between plants, in particular in the spaced pattern, where plants have no direct neighbours. In this sense, the differences of the effect of planting patterns on the MATI and curves of infection were more related with a planting aggregation threshold (or a minimal distance between plants) than with the spatial arrangements *per se*. Moreover, a low I_0 increases the time it takes to reach the maximum peak of infection at the plant level and plot level, due to delays in the start of the growth phase (Figs. 4 and 5). The time lag differences reported in sites with similar phenological timing (Li et al., 2022) can thus be explained by differences in the initial infection and planting arrangements, and not only by the positive correlation between fruit charge and plant susceptibility to infection (Avelino et al., 1993; Salgado et al., 2008). Finally, we found that high infected leaf-fall rate (γ) strongly affects the whole-plot infection dynamics and we hypothesise that this quantity is a key aspect for coffee-rust monitoring or intervention at the plot scale (Park et al., 2001).

These results have a practical significance regarding coffee rust management. They highlight the importance of reducing rust dispersal rates, either by having other trees in the plot or by planting coffee plants at larger distances (independently of the spatial arrangement *per se*) in order to uncouple individual dynamics and reduce plot infection. In particular, one should avoid the aggregated arrangement, this is, $\langle H \rangle$ values larger than 1.5 (Fig. S1.4; Video S4). This result complements those of Hajian-Forooshani and Vandermeer (2021), who tested different critical dispersal distances between coffee plants and reported that the regularity of the planting arrangement pattern modulates the time to reach fully rust-infected coffee plots. This is relevant for farmers, who balance their planting density according to their production necessities and the risk of plot epidemic (Ehrenbergerová et al., 2018). In general, conventional coffee management produces very densely aggregated planting patterns that might be prone to coffee-leaf rust invasion, contrarily to more rustic or ecological coffee plantations that intercalate different kinds of trees between the coffee plants (Moguel and Toledo, 1999). Besides, Boudrot et al. (2016) and Gagliardi et al. (2020) reported that the functional traits of plants related to shade (foliage density, shade percentage) modify the relative importance of wind and rainfall in uredospore dispersal across the plot. Understanding the role of the initial infection and dispersal rate on the time lag is also relevant for rust-control procedures that rely heavily on the timing of the epidemic, such as pruning, management of shade (Boudrot et al., 2016; Liebig et al., 2019; Soto-Pinto et al., 2000), or fungicide application (Burdekin, 1964; Mulinge and Griffiths, 1974). Additionally, the leaf-fall rate of infected leaves can also be modified with management practices but may have an ambiguous effect on the maximum infection: on the one hand, farmers could decrease the maximum infection by removing and bagging away the infected leaves continuously (thus decreasing the source of new reinfections from infected leaves either on the ground or in the plant system); but on the other hand, due to the farmers' movement between the trees, removing the leaves could trigger the dispersal of uredospores by contact and further propagate the epidemic.

The present model also allows us to make recommendations on the ways coffee rust prevalence can be measured and monitored. Here we worked with the average tree infection because it is one of the more common ways of measuring coffee rust prevalence in coffee plots (Fig. 2). Nevertheless, this variable is highly dependent on the progression of the infection in the chosen plants and their degree of temporal overlap due to spatial factors (Fig. 6). Additionally, the average over trees can be an inappropriate measure for the plot infection when individual infections follow a non-normal distribution that changes during the epidemic. Even if we supposed the infection to follow a normal distribution, the mean without the variance would not be sufficient. Other ways of measuring plot infection in the field could consist in drawing spatially explicit plot infection maps (Li et al., 2022; Rosas et al., 2021; Vandermeer et al., 2018).

In our model, we considered rust dispersal from one plant to its four closest neighbours through splash and leaf-to-leaf contact. This assumption was linked to the spatial arrangements that were only significantly different in the 4-neighbour vicinity. However, in future work it will be important to consider other mechanisms and models for spore dispersal that consider an 8-neighbour range or long-range dispersal. On the one hand, it is known that changing the neighbourhood of interaction can change the probability of plot invasion (Park et al., 2001). Also, having a different dispersal rate depending on whether the plants are in contact or not, can lead to critical transitions in infection dynamics (Hajian-Forooshani and Vandermeer, 2021; Vandermeer et al., 2018). On the other hand, if we were to consider other dispersal mechanisms such as wind gusts or human action during harvesting (Becker and Kranz, 1977), the planting arrangements might play a less important role in plot infection. This is because spores would reach farther trees and attenuate the relevance of the plot geometry. In those scenarios, the amount of shade-trees that can act as wind barriers would be crucial to reduce dispersal (Gagliardi et al., 2020) and uncouple the individual tree infection dynamics. Moreover, the model considers only one initially infected tree located in the centre of the plot. Other choices should not qualitatively change our results, but might have an effect on the general times of infection. The effect of multiple sources of infection should also be studied in future works. It is also important to keep in mind that our model assumes that infected fallen leaves are removed from the system (bagged away, for example) and cannot spread infection to neighbouring plants or reinfect. In many sites, these fallen leaves with spores likely contribute in a meaningful way to infecting plants (Zachary Hajian-Forooshani, personal obs). This could be added in the future by defining an additional R compartment in the SIX equation. Nevertheless, as coffee leaf rust is a biotroph, the survival of spores in the fallen leaves is expected to be limited.

Weather covariates like high rainfalls might also influence plant-level parameters such as the recruitment of spores from infected leaves (α) by washing off spores from the leaves. This is likely to strongly affect the general dynamics of infection (e.g. reducing the maximum infection; Figs. 2 and S1.7; Motisi et al., 2022) and should be considered in future works.

Finally, our model represents coffee rust infection but does not assess coffee production reduction. This relationship is not necessarily linear and must be considered for any practical recommendations (Cerda et al., 2017).

Control and management practices of coffee rust disease have commonly underestimated the role of dispersal and the relationship between plant and plot dynamics. Our work contributes to a better understanding of this relationship and can be used as a null-model to study the role of specific dispersal mechanisms, such as wind, splash or human mobility (see for example, Avelino et al., 2012; Becker and Kranz, 1977; Gagliardi et al., 2020; Hajian-Forooshani and Vandermeer, 2021). It mostly aimed at exploring the general and qualitative mechanisms behind the patterns observed in real systems (Fig. 2). Adding context-specific conditions would enable us to do some data-fitting and quantitative comparisons in a more detailed way than the general times of MATI and time to MATI presented here.

Recreating and understanding the main mechanisms of coffee rust dispersal is crucial to the development of a preventive approach to epidemics. It informs the management processes that seek to balance the different effects that some practices have on the infection and dispersal stages, in order to design resilient agroecological coffee systems to coffee rust or other epidemics.

CRediT authorship contribution statement

Emilio Mora Van Cauwelaert: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft. **Cecilia González González:** Methodology, Software, Visualization, Writing – review & editing. **Denis Boyer:** Conceptualization, Methodology, Formal analysis, Software, Writing – review & editing. **Zachary Hajian-Forooshani:** Methodology, Validation, Visualization. **John Vandermeer:** Formal analysis, Writing – review & editing. **Mariana Benítez:** Conceptualization, Methodology, Funding acquisition, Supervision, Visualization, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

All code and data to reproduce results in the work can be accessed at https://github.com/tenayuco/dispersion_plant_arrangement_coffeerust_infection.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2022.110206.

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APÉNDICE IV: Agricultura, biodiversidad y diversidad cultural en paisajes campesinos: una relación de mutua determinación

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AGRICULTURA, BIODIVERSIDAD Y DIVERSIDAD CULTURAL EN PAISAJES CAMPESINOS: UNA RELACIÓN DE MUTUA DETERMINACIÓN

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1. PUNTO DE PARTIDA

Este trabajo parte de la intersección entre dos grandes problemas actuales: la crisis de pérdida tanto de la biodiversidad como de la diversidad cultural, y la incapacidad de alimentar de forma sustentable y justa a la población humana. Ambos problemas tienen raíces en un modo de producción capitalista que prioriza la generación de ganancia por encima de la soberanía alimentaria[1] y de la conservación

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[1] Por soberanía alimentaria nos referimos al derecho de los pueblos a controlar sus sistemas alimentarios, tanto a nivel regional como nacional, incluyendo los mercados, los recursos naturales, la cultura culinaria y los modos de producción. Para ello, promueve prácticas agroecológicas de producción, las cuales buscan integrar los conocimientos local y tradicional junto con el conocimiento científico (ecológico, agronómico, etc.), con el fin de incrementar la producción de alimentos y al mismo tiempo sostener una vida rural digna, conservar las diversidades genética y cultural y cuidar la fertilidad de los suelos y la biodiversidad (Chapell *et al.*, 2013; La Vía Campesina, 2003).

ambiental, ganancia que obtiene a través de la explotación humana y de los ecosistemas, y del acaparamiento de las tierras (León Hernández, 2011; Rosset y Torres, 2016). El abordaje de estos problemas implica la reivindicación de derechos humanos tan fundamentales como el derecho a una alimentación adecuada, el derecho a la identidad cultural y el derecho a un medio ambiente sano (Altieri y Toledo, 2011; CEMDA, 2017; Claeys & Edelman, 2019), mismos que han sido sistemáticamente violentados en México, sobre todo con relación a los pueblos indígenas y campesinos (CEMDA, 2014). Sin embargo, estos problemas se han abordado mayormente de manera separada, llevando a veces a que los esfuerzos para asegurar la satisfacción de las necesidades alimenticias de la población se contrapongan a las metas de conservación de biodiversidad,[2] y viceversa, haciendo parecer que son actividades incompatibles (Ojima *et al.*, 1994; Lambin *et al.*, 2000; Angelsen, 2010; Burney *et al.*, 2010).

En contraste con esta tendencia, consideramos esencial reconocer que ambos problemas son altamente interdependientes. Acorde con ello, desde la agroecología se plantea que los modos de producción y consumo humano deben ser cambiados conjuntamente, promoviendo manejos ecológicos a través de formas colectivas de acción social (Sevilla & Woodgate, 2013). Esto plantea el reto de identificar los factores e interacciones concretas que median la relación entre la actividad agrícola y la reproducción de la biodiversidad y la diversidad cultural. Existen numerosos trabajos que durante los últimos años han permitido identificar el papel de la vegetación nativa y la biodiversidad sobre distintos aspectos de los sistemas agroalimentarios, por ejemplo, sobre la incidencia de plagas o la productividad de los cultivos, la polinización y la calidad de las dietas (Burel, 1989; Chust *et al.*, 2003; Franklin & Lindenmayer, 2009; Avelino *et al.*, 2012; Poveda *et al.*, 2012; Ickowitz *et al.*, 2014; Connelly *et al.*, 2015; Karp *et al.*, 2018; Gallé *et al.*, 2019; Reis Madeiros *et al.*, 2019). En otras palabras, se han estudiado bastante los efectos de la biodiversidad sobre la agricultura. En contraste, más allá de los estudios en torno a la transformación de la cobertura vegetal (Saunders *et al.*, 1991; Turner *et al.*, 1993; Trejo y Dirzo, 2000; Lambin *et al.*, 2000), se sabe poco de los efectos de la agricultura sobre la biodiversidad. A pesar de que se ha reconocido que diferentes formas de agricultura pueden tener distintos efectos sobre la biodiversidad (Moguel y Toledo, 1999; Perfecto *et al.*, 2009), éstos han sido mucho menos documentados y entendidos, lo cual ha llevado frecuentemente a discusiones simplificadas de esta interacción (Kremen, 2015; Bennet, 2017; Ortega-Álvarez *et al.*, 2018). Menor aún es la evidencia que existe respecto a las relaciones que involucran a la diversidad cultural, la cual ha surgido y continúa recreándose en íntima relación y mutua determinación con los sistemas agroalimentarios y la biodiversidad (Boege, 2008; Toledo y Barrera-Bassols, 2008; Lyver *et al.*, 2019) (figura 1).

A continuación presentamos una síntesis de nuestra aproximación, así como algunos de los resultados obtenidos y propuestas, ante la necesidad de entender los

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[2] Por biodiversidad nos referimos a la suma de las distintas formas de vida en varios niveles de organización: intra e interespecífica, variedad de ecosistemas y variación total a nivel de paisaje (Gepts *et al.*, 2012 p. 5).

factores e interacciones concretas que median la relación entre la actividad agrícola y la reproducción de la biodiversidad y la diversidad cultural en regiones de agricultura campesina en México, es decir, en lugares donde cada familia maneja pequeñas extensiones de tierra, al menos en parte para autoconsumo, y donde utilizan combinaciones de tracción mecánica y animal, abono y fertilizantes inorgánicos, y donde siembran generalmente variedades nativas (Bellon *et al.*, 2018).

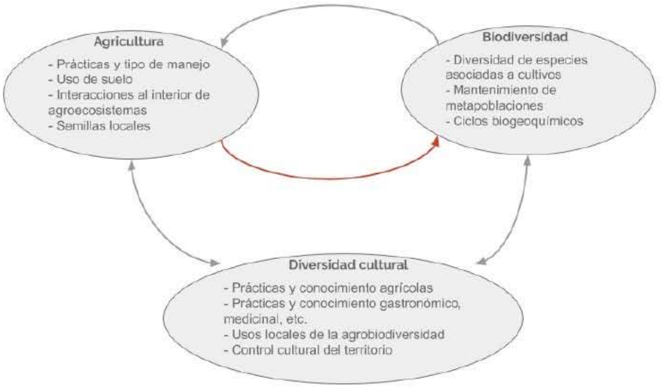

Figura 1: La biodiversidad, la diversidad cultural y la agricultura se determinan mutuamente en procesos que es necesario comprender para abordar la conservación de la diversidad biológica y cultural al mismo tiempo que se produce alimento de manera sustentable. Nuestra investigación y el presente capítulo se enfocan en entender los efectos de la agricultura sobre la biodiversidad (flecha roja).

2. EL PAISAJE AGRÍCOLA COMO ESCALA DE TRABAJO

El paisaje puede entenderse como un sistema socioecológico complejo que comprende un mosaico dinámico de usos de suelo y vegetación (Parrott y Meyer, 2012). Hemos adoptado la escala del paisaje como referente para estudiar la relación entre las actividades agrícolas y la biodiversidad porque aquí se manifiestan de forma clara sus interacciones (Ramos, 2020). No obstante, los procesos que ocurren en los paisajes no pueden desligarse de los que ocurren en otras escalas socioecológicas relevantes, como las parcelas individuales, los ejidos, las cuencas o los municipios. Los paisajes pueden caracterizarse a través de mapas que revelan el tipo y distribución de los usos de suelo y vegetación, y también a través de métricas que nos permiten cuantificar o evaluar aspectos como su permeabilidad, fragmentación, cantidad de hábitat o conectividad, entre otras propiedades (Turner, 1990; Wu, 2004; Zhang y Li, 2013; Teng *et al.*, 2016; Urrutia *et al.*, 2020). Además, es posible caracterizar el tipo de manejo agrícola y las diversidades biológica y cultural en los paisajes, lo cual resulta indispensable para diseñar estrategias integrales para abordar las aparentes contradicciones entre la producción de alimentos y la conservación de la biodiversidad (Fahrig *et al.*, 2011; Mora Van Cauwelaert, 2017; González González *et al.*, 2020; Ramos, 2020).

La importancia de la agricultura se manifiesta de forma más clara cuando notamos su ubicuidad en los paisajes del mundo. Ésta ocupa el 37 % de la superficie terrestre a nivel global y el 25 % a nivel nacional (Sánchez Colón *et al.*, 2009; Rosete-Vergés *et al.*, 2014; FAO, 2016). Es en muchos sitios la principal causa de deforestación y transformación de bosques continuos en fragmentos rodeados de una *matriz agrícola*, es decir, de un conjunto de parches de diferentes tamaños y con diferentes usos y manejos, principalmente agrícolas (Myers *et al.*, 2000; Perfecto *et al.*, 2009; Canale *et al.*, 2012; Sloan *et al.*, 2014; Tapia-Armijos *et al.*, 2015). Así, la matriz agrícola es el espacio físico donde pueden coexistir la producción agrícola, las formas de vida campesinas y la conservación de la biodiversidad, y es donde se materializa la forma en que las distintas culturas han organizado estas dos actividades (fig. 2).

3. BIODIVERSIDAD EN LA MATRIZ AGRÍCOLA: CONTRIBUCIONES DESDE LA MODELACIÓN MATEMÁTICA Y COMPUTACIONAL

3.1 Estrategias de producción agrícola y de conservación de la biodiversidad

En el ámbito de la ecología se han debatido dos estrategias contrastantes para ordenar la producción agrícola y la conservación de biodiversidad en la escala de paisaje: las estrategias de integración y de separación territorial (*land sharing* y *land sparing*, en inglés) (Ortega-Álvarez *et al.*, 2018). A grandes rasgos, la estrategia de separación territorial plantea excluir las áreas de producción de las de conservación, y procura minimizar el área dedicada a la agricultura a través de un manejo intensivo de forma que otros espacios se reserven para la conservación y la recuperación de espacios prístinos (Phalan *et al.*, 2011). En cambio, la estrategia de integración territorial propone conjuntar ambas actividades en un mismo paisaje mediante manejos agrícolas menos intensivos que minimicen su impacto sobre la biodiversidad, incluso si se destina una mayor área para la producción. Si bien esta discusión ha sido fuertemente criticada por las limitaciones de su planteamiento inicial, también ha visibilizado la importancia de comprender la interacción compleja entre la agricultura y la biodiversidad, motivando numerosos estudios teóricos y prácticos (Perfecto y Vandermeer, 2012; Ortega-Álvarez *et al.*, 2018).

Rara vez se hace explícito que las estrategias anteriores parten de diferentes supuestos sobre los efectos de la injerencia humana en los paisajes (Perfecto y Vandermeer, 2015). Por un lado, la estrategia de separación supone que la biodiversidad es muy sensible a las actividades humanas, por lo que decae súbitamente en cuanto un paisaje es alterado, de donde se deriva que para conservar es necesario mantener espacios no modificados por el ser humano. Por otro lado, la estrategia de integración supone que existe un rango de actividades poco intensivas cuyo impacto sobre la biodiversidad es mínimo, así que su pérdida ocurre lentamente y

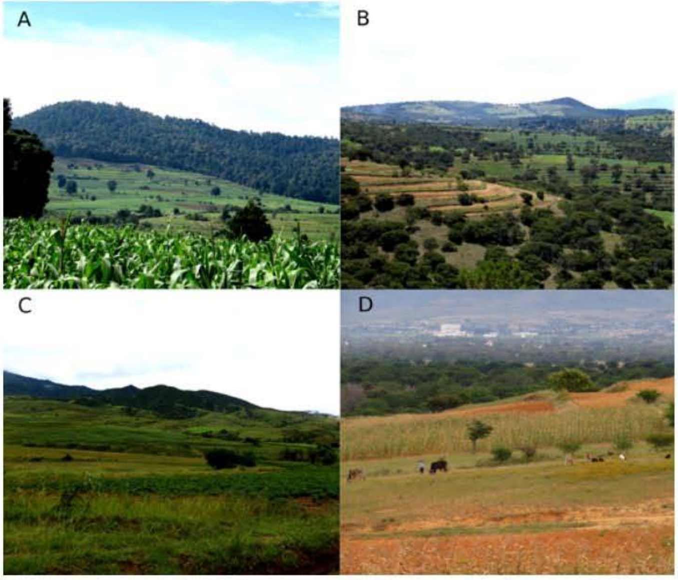

Figura 2: Matrices agrícolas en el centro y sur de México: paisajes fragmentados en los que la agricultura campesina ocupa un área importante y coexiste con diversos tipos de uso de suelo y vegetación. Fotografías de Nanacamilpa, Tlaxcala (A), Vicente Guerrero, Tlaxcala (B) y Zaachila, Oaxaca (C y D).

sólo cuando se han alcanzado altos niveles de alteración en los paisajes. Si bien se ha generado mucha información en torno al debate entre separación e integración territorial, estos supuestos no han sido puestos a prueba y la evidencia disponible hasta ahora es contradictoria (Kremen, 2015, Ortega-Álvarez *et al.*, 2018).

3.2 Probando supuestos con modelos de metacomunidades en paisajes hipotéticos

Para poner a prueba la relación entre la pérdida de biodiversidad y los cambios en los paisajes, es conveniente considerar la teoría de metapoblaciones (Levins, 1969; Hanski y Gaggiotti, 2004). Ésta plantea que las poblaciones no están aisladas, sino que forman parte de una red de poblaciones locales dispersas en el espacio, conectadas entre sí por medio de la migración de individuos entre ellas; a este conjunto de poblaciones se le llama metapoblación. Al moverse a través del paisaje, los individuos de una población local pueden recolonizar sitios donde otra ha desaparecido, ya sea por causas naturales o por disturbios antropogénicos, evitando así la extinción a nivel regional (figura 3). La dinámica de metapoblaciones es particularmente relevante en ambientes donde las poblaciones habitan en paisajes fragmentados, como los que predominan en los trópicos y subtrópicos en la actualidad (Hansen *et al.*, 2013). Si reconocemos que la migración entre parches es indispensable para evitar las extinciones regionales, entonces se vuelve clara la importancia del espacio donde ésta ocurre, es decir, la matriz agrícola (Vandermeer y Carvajal, 2001). Por tanto, dos aspectos fundamentales de la matriz son su *permeabilidad*, es decir, qué tanto facilita el tránsito o el establecimiento de especies locales, y su *estructura* o arreglo espacial, el cual también determina qué tan fácilmente las especies locales pueden migrar y recolonizar parches (Perfecto *et al.*, 2009, Papaïx *et al.*, 2015). Cabe mencionar que ambas, la permeabilidad y la estructura, dependen fuertemente del tipo de agricultura que se practique en una región. Por ejemplo, es de esperarse que las parcelas en las que no se aplica insecticida sean más permeables al tránsito o establecimiento de los insectos que en las que éste se aplica sistemáticamente. También, el tamaño de los predios en los que se realiza la agricultura afecta la estructura de la matriz. Los modelos matemáticos pueden ser de gran utilidad para simular diferentes tipos de matrices y explorar cómo responde la biodiversidad ante cambios en los paisajes. A continuación ilustramos el uso de modelos en esta dirección.

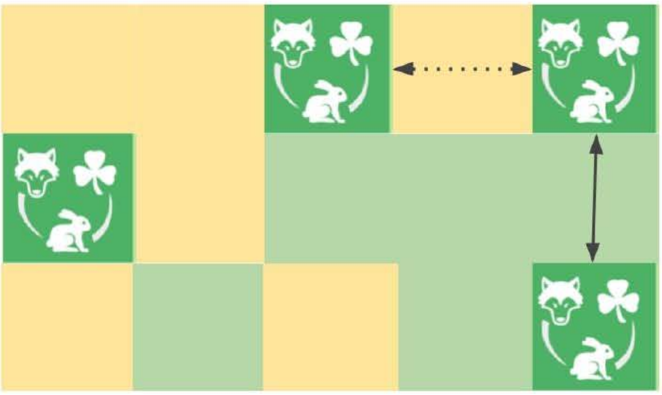

Figura 3: Las metapoblaciones se mantienen regionalmente gracias a la migración y recolonización de parches en los que pueden ocurrir extinciones locales. La imagen es una representación simplificada de una comunidad de tres especies que habitan en remanentes de bosque (cuadros verde oscuro) y que pueden migrar a través de parches de uso agrícola con una permeabilidad mayor (cuadros verde claro) o menor (cuadros amarillos). La permeabilidad y estructura de estas matrices determinan en buena medida la supervivencia de las especies en la escala regional.

Desarrollamos un modelo con el cual simulamos la distribución de comunidades ecológicas en paisajes agrícolas (figura 4A). Utilizamos el modelo de nicho (Williams y Martínez, 2000) para generar comunidades hipotéticas con estructuras realistas, compuestas por especies que se relacionan entre sí mediante interacciones tróficas. Las especies se ubicaron en un paisaje simulado compuesto por fragmentos de hábitat dispersos en una matriz agrícola. En particular, las especies se establecían en los parches de hábitat y los individuos migraban a través de la matriz, formando una metacomunidad (González González *et al.*, 2016; Ramos *et al.*, 2018a). Con este modelo, estudiamos el efecto de cambios en la permeabilidad y en la estructura de la matriz agrícola sobre la supervivencia de las especies.

Los cambios en la permeabilidad los modelamos mediante el reemplazo paulatino de parches más permeables por parches menos permeables, simulando un aumento en la intensidad de las actividades agrícolas (González González *et al.* 2016). Además probamos el efecto de la fragmentación del hábitat modificando la cantidad de parches en que se dividía una superficie constante de hábitat (Ramos *et al.*, 2018) (figura 4B). En general, encontramos que la riqueza de especies disminuye conforme la matriz pierde permeabilidad, pero la intensidad de esta disminución depende del arreglo espacial de los parches de hábitat, de la cantidad de hábitat y de las características intrínsecas de las especies (figuras 4C y 4D). Por lo tanto, encontramos que no existe una única forma en la que se pierde la biodiversidad a medida que se transforman los paisajes, sino que la pérdida depende de la interacción entre diversos factores del paisaje y de las comunidades. Esto contrasta con los supuestos tanto de las estrategias de integración como de separación territorial, ya que nos brinda evidencia matizada sobre los contextos donde la biodiversidad puede presentar una respuesta más o menos robusta a las actividades agrícolas.

4. ¿CÓMO ES LA MATRIZ AGRÍCOLA EN UN UN PAISAJE CAMPESINO? EL CASO DE ZAACHILA, OAXACA

En la sección anterior presentamos evidencia proveniente de modelos matemáticos que sugiere que diferentes rasgos de la estructura de un paisaje pueden influir en la respuesta de la biodiversidad ante las actividades agrícolas y, por tanto, en su conservación. Estos estudios sacan provecho de las herramientas de modelación para explorar paisajes hipotéticos, las cuales brindan una comprensión más detallada de las relaciones causales entre sus componentes. Sin embargo, aunque valiosos por su generalidad, los modelos presentados no dicen mucho sobre paisajes específicos, los cuales suelen ser bastante más intrincados y complejos que aquéllos modelados computacionalmente.

Los estudios de caso pueden aportar una perspectiva local y particular que complementa la generalidad de los modelos matemáticos y abonan evidencia para la discusión de estrategias conjuntas de conservación y producción agrícola en un contexto concreto. En particular, presentamos estudios de caso que nos permiten entender mejor cuál es la estructura y permeabilidad de distintos tipos de matrices agrícolas.

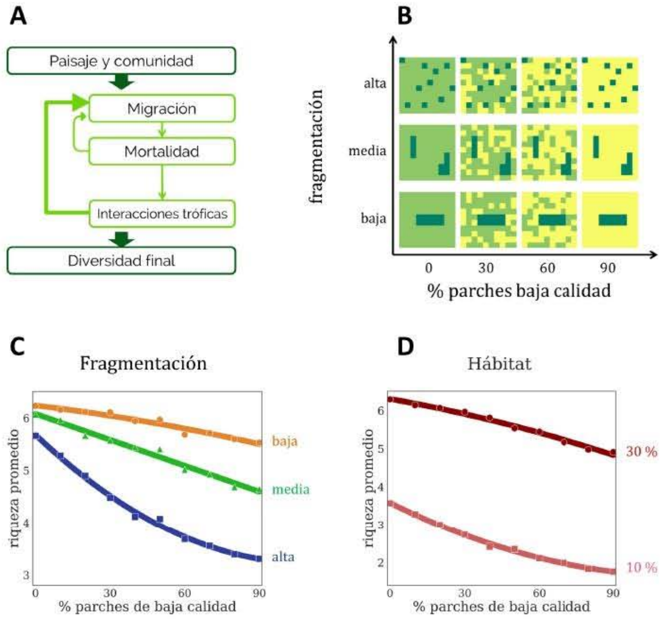

Figura 4: Esquema del modelo que acopla una dinámica de interacciones tróficas locales con la migración de individuos a través de un paisaje simulado (A). Conjunto de paisajes en los que probamos el modelo para estudiar el efecto de la pérdida de permeabilidad y la fragmentación (B). Encontramos que hay una pérdida de riqueza más abrupta cuando la fragmentación es alta (curva azul en C) y cuando hay una poca cantidad de hábitat natural (D) (Ramos *et al.*, 2018b).

Durante los últimos cinco años nuestro grupo ha trabajado en la Villa de Zaachila (Zaachila de aquí en adelante), en los Valles Centrales de Oaxaca, México. Zaachila es una pequeña ciudad, cercana a la capital de Oaxaca, con una tradición campesina de cerca de 3500 años, que históricamente ha alojado una enorme diversidad, tanto biológica como cultural (Ruiz Medrano, 2011). Los principales cultivos del municipio son el maíz (Bolita), el frijol, el cacahuate, la alfalfa y la nuez (OEIDRS, 2005). La alfalfa se siembra usualmente en terrenos con acceso a riego y es de los cultivos mejor pagados. La nuez, el frijol, el cacahuate y el maíz se suelen sembrar en terrenos de temporal y son comercializados por los mismos campesinos desde sus casas o en la plaza. El mercado de Zaachila es una de las instancias más importantes para la comunidad, es esencial para la economía campesina y constituye una interfaz entre el medio rural y el urbano (Mora Van Cauwelaert, 2017).

Además de ser de interés por su propia historia, Zaachila puede fungir como un sitio de referencia que represente a otras regiones del centro y sur de México, en donde los paisajes hayan sido moldeados mayormente por la agricultura campesina y en donde actualmente coexistan diferentes tipos de manejo agrícola y formas de tenencia de la tierra, incluyendo ejidos, tierras comunales y propiedad privada (Mora Van Cauwelaert, 2017). Además, Zaachila pasó de tener una cobertura urbana de 3 % en 2002 al 20 % en 2016, urbanizando en particular terrenos destinados a la agricultura de temporal (INEGI serie III, 2002; INEGI serie VI, 2016). En este sentido, puede ser también un sitio que permita estudiar los efectos de cierto tipo de urbanización sobre diferentes rasgos del paisaje y sus consecuencias para la biodiversidad.

4.1 Estructura espacial de una matriz agrícola campesina

Las características estructurales de los paisajes como la forma y el tamaño de los parches, la densidad de los bordes y la distancia entre los parches, también pueden tener efectos importantes en la dinámica de las metapoblaciones, en la estructura de la comunidades o en la selección de caracteres evolutivos (Tscharntke *et al.*, 2012; Melo *et al.*, 2013; Fahrig, 2017). Por ejemplo, Liao y colaboradores (2016) encontraron que ciertas configuraciones pueden compensar la pérdida de hábitat y reducir los riesgos de extinción. Desde la perspectiva agrícola, existen estudios que demuestran que el tipo de paisaje que rodea las zonas agrícolas tiene un fuerte impacto en la polinización, la herbivoría, la fertilidad y la productividad de las parcelas (Fahrig, 2003; Tscharntke *et al.*, 2005; Poveda *et al.*, 2012; Connelly *et al.*, 2015; Boesing *et al.*, 2017).

En particular, el estudio de la heterogeneidad espacial brinda herramientas formales para describir los paisajes con más claridad. La heterogeneidad espacial estudia qué compone al paisaje y cómo está estructurado en el espacio, es decir, su heterogeneidad composicional y configuracional, respectivamente (Fahrig *et al.*, 2011; Turner y Gardner, 2015). Para estudiar la heterogeneidad de los paisajes podemos utilizar distintas herramientas. Los mapas de uso de suelo y vegetación caracterizan de manera visual y cualitativa la heterogeneidad espacial, mientras que las métricas del paisaje nos permiten cuantificarla a partir de imágenes satelitales, que son cada vez más accesibles (McGarigal y Cushman, 2002).

En América Latina se han realizado pocos esfuerzos por caracterizar la estructura de los paisajes agrícolas campesinos, que son los más ampliamente distribuidos en el territorio mexicano (CEMDA, 2017; Bellon *et al.*, 2018). Debido a su prevalencia y su relación con las diversidades biológica y cultural, es necesario estudiar estos paisajes, cuyas historias de manejo son muy distintas a las de los paisajes agrícolas bajo manejo industrial descritos, con mayor frecuencia, en la literatura (McGarigal y Cushman, 2002). En nuestro grupo nos hemos propuesto sistematizar la información sobre la cobertura vegetal y el uso de suelo del municipio de Zaachila, caracterizar la heterogeneidad espacial de este sitio utilizando métricas del paisaje y proveer de elementos para delinear estrategias articuladas de conservación y producción en la zona de estudio (Urrutia *et al.*, 2020).

En cuanto a la composición del paisaje, hemos reportado que el uso de suelo agrícola es por mucho el más abundante en Zaachila, siendo la agricultura de temporal, en términos de extensión, más importante que la agricultura de riego (39 % vs. 9 %) (figura 5). La agricultura de temporal es aquella en donde sólo se siembra la parcela durante la temporada húmeda del año, pues, al no tener riego, la producción de las parcelas depende exclusivamente del agua de lluvia. Por otro lado, la agricultura de riego en esta zona es diferente a la que se practica en el norte del país o en otras zonas del mundo con sistemas altamente industrializados: el 46 % del riego en Oaxaca es riego por gravedad o riego manual (por ejemplo, a través de canales de tierra). Del resto de la agricultura de riego, el 32 % utiliza sistemas de goteo, y el 10 % sistemas de aspersión (INEGI, 2017). Esta diversidad de estrategias de riego se conjunta con la de otras prácticas agrícolas para dar lugar a una vasta diversidad de estrategias de manejo a lo largo de un gradiente de industrialización que más adelante detallaremos.

Además hemos caracterizado la heterogeneidad espacial de este paisaje mediante ocho métricas a nivel del paisaje y otras ocho a nivel de clases de usos de suelo. Esto nos permitió compararlo con otros paisajes agrícolas y argumentar en torno a los esquemas de conservación pertinentes para la zona de estudio (Urrutia *et al.*, 2020). En particular, comparamos el paisaje de Zaachila con otros paisajes agrícolas al Oeste de Estados Unidos. Encontramos que tienen diferencias importantes, atribuibles a sus distintas historias climáticas, políticas, culturales y de manejo (Cardille *et al.*, 2005). El paisaje de Zaachila, y probablemente muchos otros paisajes campesinos en nuestro país, tiene una mayor diversidad, complejidad y conectividad que los paisajes agrícolas en Estados Unidos (Urrutia *et al.*, 2020). Éste es un buen ejemplo de las diferencias que pueden existir entre los paisajes en zonas agrícolas de América Latina, manejados por campesinos, y los paisajes agrícolas que han sido el foco de los estudios de heterogeneidad del paisaje agrícola hasta el momento (Wu *et al.*, 2002; McGarigal y Cushman, 2002; Wu, 2004; Peters *et al.*, 2007; Poveda *et al.* 2012; Connelly *et al.* 2015). Así, esta comparación destaca la importancia de estudiar y caracterizar paisajes en los trópicos para poder entender los procesos socioecológicos que ahí ocurren y, en última instancia, discutir y diseñar estrategias acordes al contexto local.

De las distintas clases de uso de suelo y vegetación de Zaachila, el bosque y la agricultura de temporal son las más importantes para discutir estrategias de integración de la producción agrícola y la conservación de la biodiversidad. Por una parte, los parches de agricultura de temporal están en contacto con la mayoría de las otras clases. En contraste, el bosque está concentrado en pocos parches grandes con menos contacto con el resto de la matriz que la agricultura de temporal (figura 5). Teniendo en cuenta que los parches de bosque en general están separados unos de otros y que esto puede dificultar la dinámica de la migración y la recolonización de las metapoblaciones, la matriz que rodea los parches de bosque se vuelve central para la conservación de las metapoblaciones silvestres.

La alta heterogeneidad del paisaje de Zaachila nos habla de un paisaje complejo que puede tener efecto en la conservación de las metapoblaciones locales. Considerando la larga historia de uso de suelo agrícola de los Valles Centrales de Oaxaca y la importancia de la agricultura para la vida cotidiana de estas zonas, una propuesta viable para favorecer las conexiones entre los parches de bosque es propiciar prácticas agrícolas que favorezcan la permeabilidad en la matriz; por ejemplo, la incorporación de un arreglo diverso de cultivos, el poco o nulo uso de insumos tóxicos y una estructura espacial diversa en las parcelas capaz de dar refugio o sustento a la biodiversidad local. Dado que la matriz en Zaachila está dominada por la agricultura de temporal, que a su vez mostró tener una alta conectividad, es particularmente importante mantener y fomentar en esta clase de uso de suelo las prácticas agrícolas con estas características (Vandermeer y Perfecto, 2007; Urrutia *et al.*, 2020).

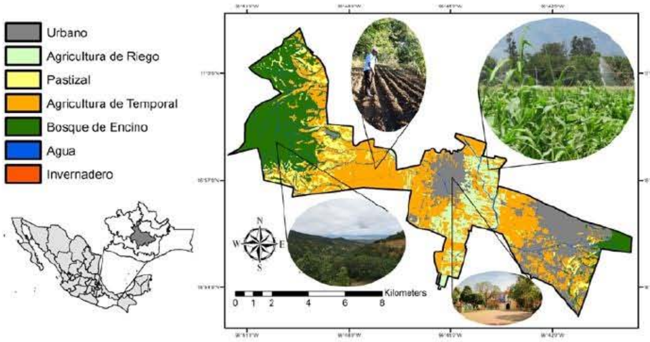

Figura 5: Diversidad de usos de suelo y vegetación y arreglo espacial de la matriz agrícola en la Villa de Zaachila, Oaxaca. Aquí, como en otros paisajes campesinos de México, la agricultura ocupa un área importante y se entremezcla en patrones intrincados con otros tipos de uso de suelo y vegetación.

4.2 Permeabilidad de los tipos de manejo agrícola: la artropofauna como indicador

En el enfoque clásico de la conservación se considera a la agricultura como gran antagonista de la biodiversidad pues se tiene en mente un tipo de manejo particular, cuyos efectos son devastadores sobre los recursos hídricos, el suelo, las especies y sus interacciones (Carson, 2002; Hobbelink, 1991). Sin embargo, no existe una sola agricultura, sino una vasta diversidad de tipos de manejo de los agroecosistemas, y que podemos ubicar a lo largo de un gradiente que va desde lo que hemos llamado tradicional hasta lo industrializado.

Entre otras cosas, los tipos de manejo se diferencian por la diversidad de especies cultivadas y asociadas; estas últimas se refieren a las especies que los campesinos no colocan en sus parcelas, pero que pueden migrar a través de ellas o establecerse temporal o permanentemente. Los manejos más tradicionales suelen tener una alta variedad de especies cultivadas y asociadas, mientras que los manejos industrializados tienen una baja diversidad de especies (Moguel y Toledo, 1999; Perfecto *et al.*, 2009; Vandermeer, 2011). De hecho, los agroecosistemas pueden fungir como importantes repositorios de vida silvestre dados ciertos tipos de manejo, por ejemplo, los cafetales agroecológicos pueden mantener y hasta incrementar la biodiversidad a nivel del paisaje. Esta diversidad de especies, a su vez, depende del resto de las prácticas llevadas a cabo en las parcelas, que en su conjunto dan lugar a su nivel de permeabilidad (Perfecto *et al.*, 1997; Perfecto, 2003; Perfecto y Armbrecht, 2003; Perfecto *et al.*, 2007).

Para estudiar cómo distintas prácticas agrícolas afectan la permeabilidad de las parcelas a la biodiversidad local de la Villa de Zaachila, comparamos la diversidad de coleópteros en parcelas con distintos tipos de manejo (González González *et al.*, 2020). Entre otras cosas, elegimos los coleópteros como grupo indicador de la permeabilidad debido a su alta diversidad taxonómica y funcional, además de su ubicuidad y los diferentes requerimientos ecológicos que las distintas familias presentan, siendo algunas generalistas y resistentes a los cambios ambientales y otras especialistas sensibles a las perturbaciones (Holland, 2002; Ohsawa, 2010; Campanelli & Canali, 2012; Lassau *et al.*, 2005).

Caracterizamos el tipo de manejo con base en una metodología mixta que combina información obtenida de entrevistas hechas a los campesinos y observaciones en campo con estadística multivariada (Alvarez *et al.*, 2014). Para ello, trabajamos con un grupo de campesinos con quienes hemos construido una relación de confianza a través de los años de trabajo conjunto en la localidad. Juntos, hicimos una primera búsqueda de parcelas con características contrastantes. Por un lado, buscamos parcelas con una alta variedad de cultivos, preferentemente de semillas locales, y con un nulo o bajo uso de insumos agroindustriales. Aunque la combinación exacta de prácticas agrícolas variara entre ellas, postulamos que al compartir estas características constituirían una categoría similar. Por otro lado, buscamos parcelas que tendieran a la siembra de variedades híbridas en monocultivo y al uso de maquinaria pesada.

Con esto en mente, los campesinos nos ayudaron a elegir dieciséis parcelas distribuidas al norte, sur, este y oeste de la localidad. Tras esta primera selección, realizamos una descripción más detallada del manejo de las parcelas a través de observaciones *in situ* y de entrevistas semiestructuradas. Las entrevistas fueron dirigidas al núcleo familiar responsable del manejo de cada parcela y trataron temas como las especies sembradas, el origen de sus semillas, el uso de insumos externos, las técnicas de rotación de cultivos, los métodos de deshierbe, la presencia de quelites, los cercos vivos, la presencia o ausencia de riego, la incorporación o no de la cosecha al mercado, etc. De toda la información recabada y sistematizada, se eligieron las variables para las que obtuvimos información clara por parte de todos los entrevistados. Éstas se integraron en un análisis de componentes principales que dio como resultado un gradiente de industrialización a lo largo del cual se ubicaron las parcelas muestreadas. Para facilitar el análisis, discretizamos este gradiente en dos categorías: las parcelas tradicionales y las industrializadas. Cabe resaltar que el nivel de industrialización es relativo, pues todas conservan rasgos de la agricultura campesina tradicional, como el tamaño pequeño de las parcelas y su manejo fundamentalmente familiar. A partir de este análisis encontramos que las variables que definieron con más peso el gradiente de industrialización fueron la cantidad de cultivos presentes y la cantidad de variedades de cada cultivo. Esto quiere decir que en esta localidad, el resto de las variables que generalmente han sido asociadas al manejo tradicional (por ejemplo, variedades nativas, presencia de quelites, árboles y bordes manejados (Altieri *et al.*, 1997)) suelen encontrarse presentes en aquellas parcelas con una alta diversidad de cultivos. La presencia o ausencia de riego, por otro lado, no fue una variable definitoria para ninguna de las dos categorías de manejo.

De acuerdo a esta categorización, encontramos que la diversidad de coleópteros, tanto a nivel de familias como de morfoespecies, fue significativamente mayor ($p < 0.05$) en las parcelas del grupo tradicional. Además, encontramos una correlación positiva entre la diversidad de la familia Curculionidae (conocidos localmente como gorgojos o picudos) y el resto de los coleópteros, así como una correlación de la misma con los manejos más tradicionales. Debido a estas correlaciones y a la ubicuidad de los curculiónidos en la mayoría de las parcelas, parecen ser un indicador útil en la zona para evaluar la permeabilidad de las parcelas. Así pues, los distintos tipos de manejo agrícola en la Villa de Zaachila sí tuvieron un efecto significativo sobre la permeabilidad de las parcelas y por lo tanto en su biodiversidad asociada. Sumando este resultado con el análisis sobre la heterogeneidad espacial del paisaje de Zaachila, postulamos que fomentar un tipo de manejo tradicional en las zonas de agricultura de temporal es una manera óptima de mejorar la permeabilidad del paisaje y, por tanto, beneficiar la conservación de la biodiversidad en el mismo.

4.3 Los modos de producción agrícola y la diversidad cultural

Los tipos de manejo agrícola, y en última instancia la matriz agrícola, son construidos y modificados por las comunidades campesinas. Los campesinos son el resultado de lo que producen y cómo lo producen. En las milpas, los traspatios y los bosques, la naturaleza es transformada por el ser humano y es transformadora de éste al mismo tiempo. Es ahí donde los campesinos van fabricando significados y construyendo una identidad. La vida de los campesinos se concretiza en el campo de cultivo y es éste el medio en donde se han ido materializando un gran número de relaciones sociales a lo largo del tiempo. Entender las interacciones económicas, históricas y culturales que atraviesan las comunidades campesinas nos puede dar más pistas sobre cómo realizar una agricultura justa socialmente que al mismo tiempo conserve la biodiversidad (fig. 1). Por ello, de manera paralela hemos explorado algunas determinantes de esta dimensión y sus implicaciones en la relación agricultura-biodiversidad (Foster, 2000; Lefebvre, 2013; Mora Van Cauwelaert, 2017; Alonso-Fernández, en preparación).

A través de entrevistas con las familias campesinas encontramos que el manejo tradicional de la milpa en Zaachila, y en particular la siembra de maíces nativos, está siendo desplazada por la siembra de variedades híbridas y por la importación de granos de maíz de otros estados como Sinaloa o Puebla. Por un lado, la siembra de maíces híbridos y los paquetes de agroquímicos suelen prometer una salida económica más rentable, llevando a varios campesinos a optar por una agricultura más industrial. Por otro lado, el bajo precio del maíz importado desmotiva la siembra local de maíces nativos. A pesar de esto, la siembra de maíces nativos se ha logrado mantener en varias familias por sus usos en la elaboración de platillos específicos, para fiestas o eventos en diferentes momentos del año. En efecto, el maíz tipo *Bolita* en sus diferentes subtipos (blanco, amarillo, rojo) se emplea para elaborar una gran variedad de comidas (figura 6). Los sabores y texturas de estos maíces, pero también los tiempos de cocción y preparación, son buscados por las mismas personas de la comunidad. Por ello, el maíz nativo sigue siendo esencial en las familias en Zaachila y, aun con precios de venta más elevados, sigue siendo comprado y, por lo tanto, resembrado cada año (Mora Van Cauwelaert, 2017).

Es así que la siembra de maíces nativos, el manejo tradicional asociado y su impacto sobre la biodiversidad son afectados por determinantes económicas, pero también por la cosmovisión de la comunidad. La agricultura es, por lo tanto, un hecho político en cuanto a que es ahí donde se reproducen las relaciones sociales de producción y donde se tiene la conciencia y la capacidad de incidir sobre la realidad. La diversidad asociada a los agroecosistemas es producto de la sociedad, y consecuencia del trabajo que durante miles de años se ha ido concretando y materializando tanto en las variedades de plantas producidas en el presente como en las recetas y en las fiestas de la comunidad. Es así que las milpas, los traspatios y los bosques, y finalmente el paisaje, son el lugar en donde se produce un amplio conjunto de objetos naturales y sociales; objetos que no sólo son cosas sino que son, sobre todo, relaciones (Foster, 2000; Brush & Perales, 2007; Urquijo y Barrera-Bassols, 2009; Alonso-Fernández, en preparación).

5. CONCLUSIONES, APRENDIZAJES Y PERSPECTIVAS

Comenzamos este capítulo argumentando que la biodiversidad, la agricultura y la diversidad cultural se determinan y retroalimentan entre sí de diferentes maneras (figura 1), de forma que abordar los problemas asociados a la pérdida de biodiversidad y la prevalencia de sistemas agroalimentarios no sustentables requiere de marcos de referencia integrales. En particular, las ciencias de la complejidad proveen de un marco conceptual y técnico para abordar el estudio de sistemas caracterizados por interacciones bidireccionales y no aditivas entre diversos elementos, así como para modelar y explorar las dinámicas espacial y temporal de sistemas de este tipo, como son los sistemas agroalimentarios (e.g., López-Martínez, 2017; Braasch *et al.*, 2018; García Jácome *et al.*, 2020).

Figura 6: Variedad de platillos como ejemplo de la diversidad cultural asociada a la agricultura campesina y las variedades locales de maíz y otros cultivos. A. Tamales, B. Nicuatole, C. Memelas, D. Atole, E. Tlayuda, F. Pinole, G. Tejate, H. Espuma, I. Tortillas. Las imágenes A, C, D, E y G son de dominio público. La imagen H proviene de la Feria del Atole y la Espuma. Las imágenes B, F e I fueron tomadas por Emilio Mora Van Cauwelaert.

En nuestro caso, la perspectiva de las ciencias de la complejidad nos ha permitido conceptualizar el sistema de relaciones entre la biodiversidad, la agricultura y la diversidad cultural, en general, y también en un caso concreto en los Valles Centrales de Oaxaca (figura 1). Esta conceptualización nos ha guiado en el diseño de investigaciones teóricas y prácticas orientadas a identificar los mecanismos y determinantes de este sistema, las cuales incluyen desde entrevistas y muestreos en campo, hasta la elaboración de modelos matemáticos y computacionales.

Entonces, por un lado hemos estudiado cómo son los tipos de manejo agrícola en los Valles Centrales de Oaxaca y cómo éstos se relacionan con la diversidad de los escarabajos. Los escarabajos, a su vez, son considerados un buen indicador de diversos procesos ecológicos e interactúan con los cultivos de manera importante, ya sea como herbívoros y potenciales plagas, como detritívoros o como polinizadores. Por otro lado, hemos utilizado métricas cuantitativas para estudiar la composición y configuración del paisaje agrícola en esta zona, el cual ha resultado particularmente heterogéneo. Con base en esto y en los aprendizajes generados a partir del estudio de paisajes y especies virtuales, hemos podido especular respecto a cómo la agricultura tradicional, al alojar mayor diversidad de escarabajos que la agricultura industrializada, puede fungir como una matriz que facilite la migración y la reproducción de la biodiversidad local. A su vez, las parcelas de temporal, por su ubicación clave en el paisaje, son el lugar ideal para fomentar este tipo de manejo. Finalmente, hemos documentado que una de las principales motivaciones para la siembra de variedades locales de maíz radica en su uso como parte de la amplia cultura culinaria zaachileña. En la tipología de manejos agrícolas encontramos que la siembra de estas variedades locales, sobre todo cuando es en policultivo, está asociada a un manejo agrícola más permeable para la biodiversidad local y a una matriz agroecológica de mayor calidad.

Así, conceptualizar este sistema de relaciones y explorar sus especificidades a partir de diversos métodos de la ecología y de las ciencias de la complejidad, nos ha facilitado cuestionar la falsa dicotomía entre conservación y producción de alimentos así como reconocer la multicausalidad de los fenómenos implicados. También nos ha permitido entender mejor los procesos de creación y reproducción de las diversidades biológica y cultural: cómo la reproducción de la cultura campesina, manifestada por ejemplo en la bebida conocida como tejate, va de la mano de la reproducción de las variedades nativas de maíz y de una forma de producción que favorece la reproducción de los escarabajos, y probablemente de muchos más taxones que habitan estos paisajes agrícolas. Esto resuena con la propuesta agroecológica que sostiene que para conservar las diversidades biológica y cultural del planeta, es fundamental unirse a las luchas de millones de campesinos que han creado y reproducido sistemas agroalimentarios más sustentables y justos que la contraparte del agronegocio capitalista (Perfecto *et al.*, 2009; Rosset y Altieri, 2018).

Aún queda mucho por aprender respecto a la aplicación de los modelos y aproximaciones que presentamos en este capítulo. Cada modelo expuesto tiene, además, sus propios supuestos y limitaciones, por lo que resulta fundamental contrastarlos entre sí para interpretarlos correctamente. Por otra parte, también resulta crucial compararlos y de ser posible articularlos con estudios históricos, antropológicos y sociológicos que trabajen con otros supuestos y herramientas (e.g. Braasch *et al.*, 2018; García Jácome *et al.*, 2020). Pero quizá el mayor desafío consiste en generar y utilizar este tipo de estudios a partir del trabajo conjunto con los campesinos y habitantes de las matrices agroecológicas de las que tanto hemos hablado. Nos queda por delante explorar, por ejemplo, si es posible seleccionar las variables y supuestos de los estudios no sólo a partir de la teoría ecológica o agroecológica que podemos aportar como investigadores, sino también a partir de las necesidades, intereses y conocimiento de quienes viven los territorios y construyen la biodiversidad y la diversidad cultural. Nos entusiasma pensar en las herramientas de las ciencias de la complejidad como medios para imaginar y transformar paisajes y territorios en los que puedan coexistir sistemas agroalimentarios campesinos justos con la biodiversidad en todos sus niveles y formas.

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APÉNDICE V: Linking Coleopteran Diversity with Agricultural Management of Maize-Based Agroecosystems in Oaxaca, Mexico

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Linking Coleopteran Diversity With Agricultural Management of Maize-Based Agroecosystems in Oaxaca, Mexico

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Biodiversity is known to be influenced by agricultural practices in many ways. However, it is necessary to understand how this relation takes place in particular agroecosystems, sociocultural contexts and for specific biological groups, especially in highly biodiverse places. Also, in order to systematically study and track how biodiversity responds or changes with agricultural practices, it is necessary to find groups that can be used as practical indicators. We conduct a study of beetle (Coleoptera) diversity in maize-based agricultural plots with heterogeneous management practices in the Central Valleys of Oaxaca, Mexico, a region with outstanding biodiversity and a long agricultural history. We use a mixture of local knowledge and multivariate statistics to group the plots into two broad and contrasting management categories (traditional vs. industrialized). Then, we present an analysis of Coleopteran diversity for each category, showing higher levels across different diversity indexes for the traditional plots. Specifically, Coleopteran guilds associated with natural pest control and soil conservation are more common in traditional plots than in industrialized ones, while herbivorous beetles are more abundant in the second. Also, our results let us postulate the Curculionidae family as an indicator of both management type and overall Coleopteran diversity in the agricultural lands of the study site. We discuss our results in terms of the agricultural matrix quality and its role in strategies that favor the coexistence of culturally meaningful agricultural systems and local biodiversity.

Keywords: agroecological matrix, agricultural management, typology, Oaxaca Mexico, Coleoptera (beetles)

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INTRODUCTION

Agriculture is a diverse and dynamic process that involves a large variety of production practices. These practices are not assembled at random, but occur as sets of land management activities, "management types," that are interdependent, adapted to each other and that function as a system with specific goals (Andow and Hidaka, 1989; Vandermeer, 2011). Depending on management type, agriculture can affect in different ways the maintenance of biodiversity at the local and regional level. Indeed, it has been suggested that some types of agricultural management can coexist and even favor biodiversity conservation if it allows for the temporary or permanent establishment of local species in agroecosystems (Perfecto et al., 2009; Fahrig et al., 2011; Kremen and Merenlender, 2018).

However, the relationship between specific agricultural management types with biodiversity and ecosystem services, like pest control and pollination, is not straightforward. On the one hand, agricultural landscapes can rarely be associated with a single and clear management type. In the tropics and subtropics, for example, one regularly finds patchy landscapes with mixed management types that incorporate some industrial characteristics but keep many features of traditional agriculture (Perfecto et al., 2009; Álvarez et al., 2014; Ramos, 2020; Urrutia et al., 2020). It is thus a challenge to organize such heterogeneity into typologies that allow us to test the role of management, as well as of specific agricultural practices, on the maintenance of biodiversity and its associated ecosystem services (Álvarez et al., 2014). On the other hand, the response of biodiversity to agricultural management depends on numerous factors, like the species under study, landscape structure, type of crop, climatological conditions, etc. (Lindenmayer et al., 2012; Wilson et al., 2017; Winter et al., 2018; Qiu et al., 2019). In order to overcome a simplistic view that conceives agriculture as an absolute antagonist to biodiversity, it is thus necessary to assess the effect of agricultural management in different contexts and case studies, and to identify, favor or adapt strategies that allow for its coexistence with biodiversity.

In ecological terms, agricultural managements with high planned diversity and low input dependence are usually associated with heterogeneous landscapes that enable diverse ecosystem services (Perfecto, 2003; Fahrig et al., 2011; Kremen and Merenlender, 2018; Urrutia et al., 2020). Under certain conditions, these types of agroecosystems have been shown to maintain or even increment the biodiversity at a landscape or plot level, exhibiting a high diversity of organisms that are, in turn, good indicators of overall biodiversity and ecosystem functioning (Perfecto, 2003; Gallé et al., 2019; Happe et al., 2019; Qiu, 2019). In turn, it has been suggested that the reduction of plant species in some agroecosystems leads to a decrease in the number and type of habitats suitable for associated biodiversity, including arthropods (Tylianakis et al., 2007; Letourneau et al., 2011; Fabian et al., 2013; Isbell et al., 2017; Liere et al., 2017). Such reduction in plant diversity, and the concomitant reduction in potential habitats, is often driven by industrialized managements in which plants other than the main crop are not grown and are usually not tolerated and landscape structure is simplified (Ekroos et al., 2010; Cizek et al., 2012; Karp et al., 2018).

In particular, the loss of arthropod diversity has been reported to result in the loss of key ecosystemic services, like natural pest control, pollination, or soil conservation (Bianchi et al., 2006; Cizek et al., 2012; Poveda et al., 2012; Wan et al., 2019; Flores-Gutierrez et al., 2020). Within arthropods, in this work we will focus on Coleoptera (beetles), since their diversity and abundance has been found to correlate with other vertebrate and invertebrate taxa (Pearson and Cassola, 1992; Holland, 2002; Ohsawa, 2010), as well as with with key environmental variables (Lassau et al., 2005; Campanelli and Canali, 2012) and agricultural management practices (Kromp, 1999; Holland and Luff, 2000; Burgio et al., 2015; Flores-Gutierrez et al., 2020). Beetles are cosmopolitan, they define a great variety of niches, exhibit diverse life strategies and they take part in several ecological processes making them important matter and energy flux regulators (Hunt et al., 2007; Bouchard et al., 2011). Moreover, beetles have been postulated as bioindicators of agroecosystem functioning (Pizzolotto et al., 2018), as they include both potential pests and natural pest enemies, as well as pollinators and detritivorous species, among others (Hunt et al., 2007; Brooks et al., 2012).

In spite of the key role of beetles within agroecosystems, it remains to be tested if their overall diversity and abundance, as well as that of guilds potentially involved in agroecosystem services or disservices, exhibit differences between different types of management in widely distributed maize-based agroecosystems in the tropics. Addressing this issue may also lead to the postulation of specific groups of beetles as indicators of management, overall coleopteran diversity and agroecosystem functioning in this type of agroecosystem. Maize-based agroecosystems like the Mesoamerinca *milpa*, which includes maize, beans and other plants, are fundamental in terms of: (i) food production and nutrition (e.g., Bellon et al., 2018; GIAHS-FAO, 2020), (ii) the vast cultural diversity and knowledge associated to their reproduction, as illustrated for instance in their uncountable gastronomic expressions (CEMDA, 2017; Mora Van Cauwelaert, 2017; Lyver et al., 2019; GIAHS-FAO, 2020), and (iii) their potential role in conservation in the ample and highly biodiverse areas in which they have been historically practiced (Myers et al., 2000; Oviedo, 2002; Bellon et al., 2018).

In this work, we sampled the beetle community in plots belonging to a highly heterogeneous, peasant-driven agricultural landscape (Urrutia et al., 2020). We worked in the Central Valleys of Oaxaca, Mexico, a region recognized for its extraordinary biological and cultural diversity, and that is in many ways representative of small-scale agriculture landscapes in southern Mexico (Mora Van Cauwelaert, 2017; Ramos, 2020; Urrutia et al., 2020). In the area where this study was conducted, a relatively diverse scarab beetle community has been previously described, and was found to be as rich in croplands as in contiguous forests (Ramírez-Ponce et al., 2019). Nevertheless, the relationship between agricultural management and the diversity of beetle taxons and guilds, as well as their potential ecosystemic services, had not been assessed prior to our study. Given the evidence summarized above, we expected to find a higher diversity of Coleoptera in plots with traditional practices involving relatively high plant diversity (and habitats) and little use of external inputs, such as pesticides. Within this diversity, we expected to find a better representation of guilds associated to ecosystemic services in more diversified and traditionally managed agroecosystems. We also expected to find specific taxons that could function as practical biological indicators of the management type and the overall coleoptera diversity.

METHODS

Study Area

This study was conducted at Villa de Zaachila (Zaachila hereafter), in the Central Valleys of Oaxaca, Mexico. It is a semi-urban population located 17 km southeast of the state's capital. The history of landscape management of Zaachila begins with the Zapotec peoples, about 3,500 years ago. Today, agricultural plots are mostly managed by small landholders for family or local consumption. Many of these plots represent a state-given usufruct land, the so-called *ejidos*, in which variable degrees of collective management occurs (INEGI, 2007; Mora Van Cauwelaert, 2017). The most represented land use types are agriculture, which covers 48% of its total area, secondary forest with 23% and urban zones with 19% (Urrutia et al., 2020). According to government data, the municipality is composed of 1,669 ha which are distributed among 1,521 small landholders (heads of family), which is to say every family has an average of 1 ha of land. This small-scale agricultural scheme combines very diverse practices in a rather fine-scale mosaic (INEGI, 2007; **Figure 1**). In order to organize this heterogeneous management context into types or categories that were amenable to further analyses, we used a previously reported method to generate management typologies (Álvarez et al., 2014; see Plot Categorization section below).

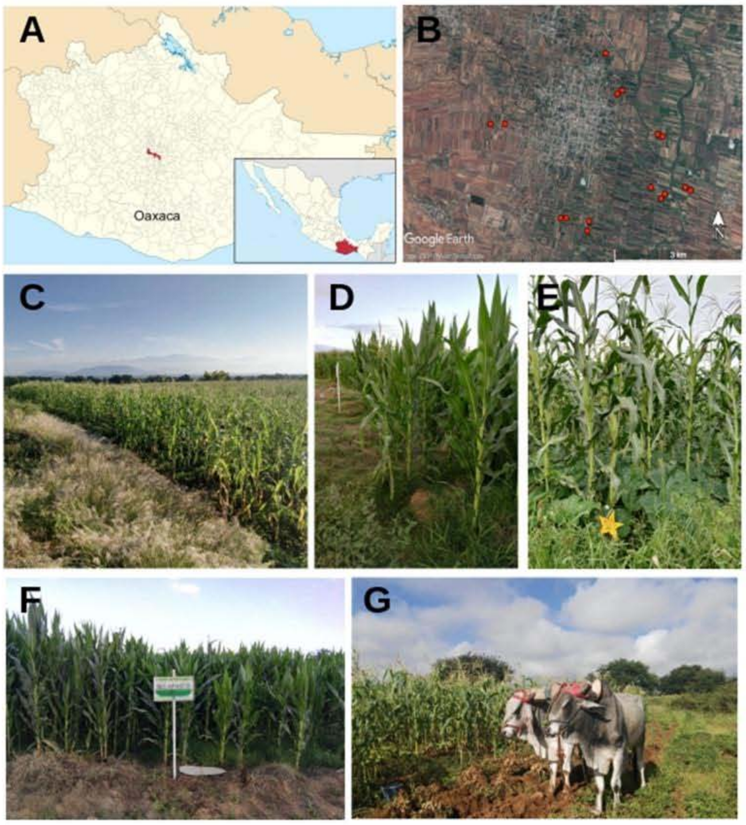

FIGURE 1 | Maize-based agricultural systems in the study site. The plots were selected in the municipality of Zaachila, Oaxaca **(A)** as neighboring pairs with contrasting types of management, as suggested by our informers **(B)**. The management practices were diverse and ranged from low-input polycultures to high-input monocultures **(C–G)**. **(D,F)** illustrates more industrialized plots in which maize is grown in monoculture and with the use of external and commercial inputs. **(C,E,G)** illustrate more traditional plots exhibiting a maize-based polyculture called *milpa*, as well as animal traction. Sources: Wikimedia commons ID 360701525 and 284784087 **(A)**, Google Earth **(B)** and personal photographs **(C,D)**.

Plot selection

Using the methodology developed by Álvarez et al. (2014), we looked for 16 plots belonging to contrasting types of management. The methodology seeks to group heterogeneous plots based upon management information provided by local key informants in a reproducible way. It starts with an initial hypothesis, in which plots that are thought to belong to qualitatively different management categories are selected by key informants. Then, thorough information about their management is obtained through interviews and, finally, a statistical multivariate test is performed in order to confirm or refute the hypothesized categorization. In the following we elaborate these steps.

During September 2016 we worked with a group of small landholders, key informants in the community who provided us information about the study site (Marshall, 1996a,b). Together, we set out to find plots belonging to two qualitatively different management types. First, a *traditional* type, characterized by a low use of commercial inputs and the planting of diverse, local seeds. Even though the exact combination of agricultural practices in each plot actually varied, we postulated that by sharing those two features they would constitute an identifiable category. Second, we looked for the *industrialized* type, which would be formed by plots with a relatively high use of machinery (for the oaxacan Central Valleys context), agrochemicals and few types of hybrid seeds. With this in mind, and according to their knowledge of local practices, the local small landholders led us to eight pairs of plots composed of what they judged was one plot under traditional management and one industrialized plot. In order to make the sample as representative as possible and to reduce biases stemming from possible landscape heterogeneities, we required plots in each pair to be as close to one another as possible (when possible even side to side) and for them to cover the North, South, East and West parts of the locality (**Figure 1**). This assignment of plots to management type represented our initial hypothesis and was later tested with a statistical analysis performed over a set of variables that were obtained from detailed interviews to the owners of each plot, as we will explain in the subsequent sections.

Plot Typology Validation

Still following the methodology by Álvarez et al. (2014), we conducted semi-structured interviews with the owners of each plot in order to collect information on their agricultural management. We asked for information about the planted crops in the current and previous years, use of industrial inputs along the year (fertilizer, pesticides, herbicides, and machinery), rotation techniques, attitude toward non-planted herbs and trees, irrigation use, purpose of the crops (such as family use or market sales), relative economic importance for the family, and so forth. The complete list of variables, definitions and data type can be read in in the **Supplementary Material** (**Supplementary Table 2**).

Interviews lasted between 1 and 2 h and they were recorded in audio and summarized in written questionnaires. Some of the variables were also systematically verified by sight in the plots, such as the presence of trees or herbs and the number of crops planted at the current time, but most were only obtainable through the interviews since they involved actions taken in the previous months or other non-observable aspects. Prior to this process, an informative letter was given to each of the participants and all of them gave their informed consent to participate in the study. Because many plots were not managed by single individuals but by families, we interviewed more than one person by plot when it was possible, mainly couples who were together in charge of the plots and households. In total, we interviewed 21 people, with ages ranging from 39 to 78 years old (average age was 60, standard deviation 10.9 years), composed of 16 men and 5 women.

Out of all the information obtained, we chose those management-related variables for which we had clear and unequivocal responses from all interviewees. Two variables (number of crops and number of crop varieties) were recorded as absolute richness values and the rest were recorded as presence/absence values. We are aware of the loss of information that this process implied but we hold it necessary for having a comparable set of data for all plots and to proceed as suggested by Álvarez et al. (2014). This gave a result of 22 variables, which were poured into a quantitative table that can be found in the **Supplementary Material** (**Supplementary Table 3**). We used this table to test the initial categorization of plots proposed jointly with key informants (traditional and industrialized). We created a correlogram of Spearman coefficients in order to look for relationships among management practices. Then, due to the type of variables in our study, we used a Factor Analysis of Mixed Data (FAMD) for organizing the plots according to their management practices. This allowed us to confirm or refute the categorization hypothesized by our key informants in order to form the groups that were later used as treatments to compare beetle diversity. All tests were done using the *FactoMineR* and *corrplot* packages from the coding language *R 1.1.383* (R Core Team, 2014). All scripts used for this investigation are publicly available at: https://github.com/laparcela/ColeopteraZaachila.

Diversity of Coleoptera

Plot extension was around 50 × 200 m, and we established five quadrants measuring 1.5 × 1.5 m in each one. In order to randomly locate the quadrants within plots, we first established a random point in each of the long sides of the plot and drew an imaginary line connecting them. At this line's center, we established the first sampling quadrant. Then we established another two quadrants halfway between this center and each of the line's extremes. Afterwards, a second imaginary line was drawn perpendicularly to the first line, crossing its center. The fourth and fifth quadrants were established at the extremes of this second line. Following this procedure, we obtained five quadrants within each plot, three at the plot interior and two at the plot borders (A diagram can be found in the **Supplementary Figure 1**). Sampling was made this way because it was done as part of a broader study and this design fitted all sampling purposes (work in preparation). Beetle collection was made before any other sampling in order to avoid disturbing individuals.

During September 2016, toward the end of the rainy season and when crops were almost ready for harvesting, all plots were sampled through the use of sweep nets in the five quadrants. Two plots were sampled each day, starting at 7:00 a.m. and until ∼11:00 a.m. This was kept constant in order to avoid extra noise from a day's normal temperature variation. Due to time limitations, we only had one sampling date per site, which represents a shortcoming for our study. Likewise, it is important to note that the use of sweep nets biases the sampling toward beetles that are active in the above-ground part of the agroecosystem, mainly on stems, leaves, flowers, fruits or sometimes flying in the air. Collected specimens were fixed with 70% ethanol and specimens from the five quadrants were pooled together in a single sample for each plot and then taken to a laboratory for identification. Individuals were identified to family level using identification keys (White, 1983; Tripplehorn and Johnson, 2005) and to morph level afterwards. Diversity was quantified as abundance and richness at both family and morph levels. The complete dataset for this investigation is publicly available at: *https://knb.ecoinformatics.org/view/urn%3Auuid%3A0b5a89ef-93f8-493c-8bff-e4843b9a45b9*.

Diversity in the industrialized and the traditional plots was compared using one-way ANOVAs, Renyi diversity analysis [using the *vegan* and *BiodiversityR* packages from the coding language *R 1.1.383* (R Core Team, 2014)] and direct quantifications at several taxonomic levels. Following the ANOVA tests, which were performed using each plot as a separate sample, we pooled all plots belonging to the industrialized group in one, and all plots belonging to the traditional group in another sample, and compared their overall richness. A Renyi diversity analysis was performed on these compound samples. Renyi's analysis relates in a graphical way many widespread ecological indexes, which are located along the horizontal axis while the vertical axis shows the corresponding value for Renyi's index (H-alpha)[1]. Afterwards, we grouped the families into four trophic guilds in order to assess functional differences between types of management. The guilds comprised herbivores, predators, detritivores, and polyphagues, the latter including cases when individuals are able to exploit a wide variety of feeding resources and cases when juveniles and adults belong to different categories. The complete table of families belonging to each guild can be found in **Supplementary Table 4** (based on the public dataset mentioned above). We also performed a Canonical Correlation Analysis (CCA) in order to test the relation between a chosen set of management variables and a set of beetle families. In order to reduce the number of variables and meet the test's requirements, we chose those management practices whose contributions to our PCA's first two dimensions were above a reference value that corresponds to the expected value if the contributions were uniform. Variance-inflation factors were calculated to eliminate variables causing multicollinearity. Additionally, we focused only on the most abundant families inside each trophic guild. This procedure left us with 8 management variables: number of crops, irrigation, quelites, trees, compost, and industrial fertilizer, pesticide and herbicide. These were tested for correlation with 9 beetle families: Cleridae, Coccinellidae, Carabidae, Chrysomellidae, Curculionidae, Nitidulidae, Anobiidae, Cantharidae, and Phalacridae.

Finally, we looked for a beetle family that could be a useful indicator of the agricultural management type. We required it to be non-exclusive of a particular type of management, but to show a clear and different response to the management categories. In order to test its potential as an indicator, we analyzed the relation between its abundance and (i) plot management and (ii) overall beetle diversity (**Figure 8B**). For this, we adjusted a second degree polynomial to its abundance in each plot (we took the natural logarithm of this measure in order to comply with the analysis assumptions) against its position along the management gradient (the coordinate each plot occupied in the horizontal axis of **Figure 3A**). We also analyzed the relation between such family's abundance and the total richness of beetles in each plot.

RESULTS

Plot Categorization

The correlogram showed relations among sets of management practices, as expected from the theoretical postulation of management types (Vandermeer, 2011; Álvarez et al., 2014). We found a positive correlation (**Figure 2**, groups of blue circles) between practices commonly associated to a traditional management, such as managed border, use of manure, animal traction, number of crops, quelites (non-planned herbs that

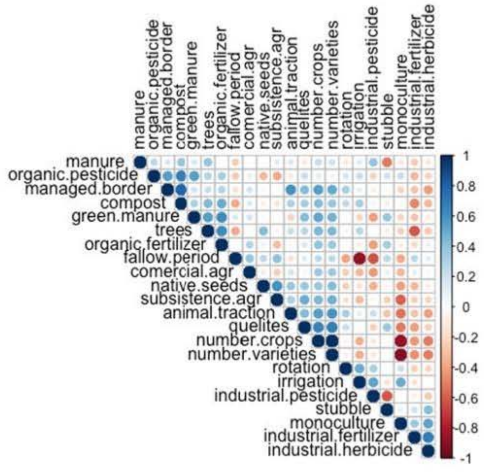

FIGURE 2 | Spearman correlation coefficients between management practices.

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[1] The equation that relates *alpha* and *H-alpha* is $H\text{-}alpha=1/(1-alpha)*log(sum(pi\wedge alpha))$. For more details, look at the work by Tóthmérész (1995) and Jost (2006).

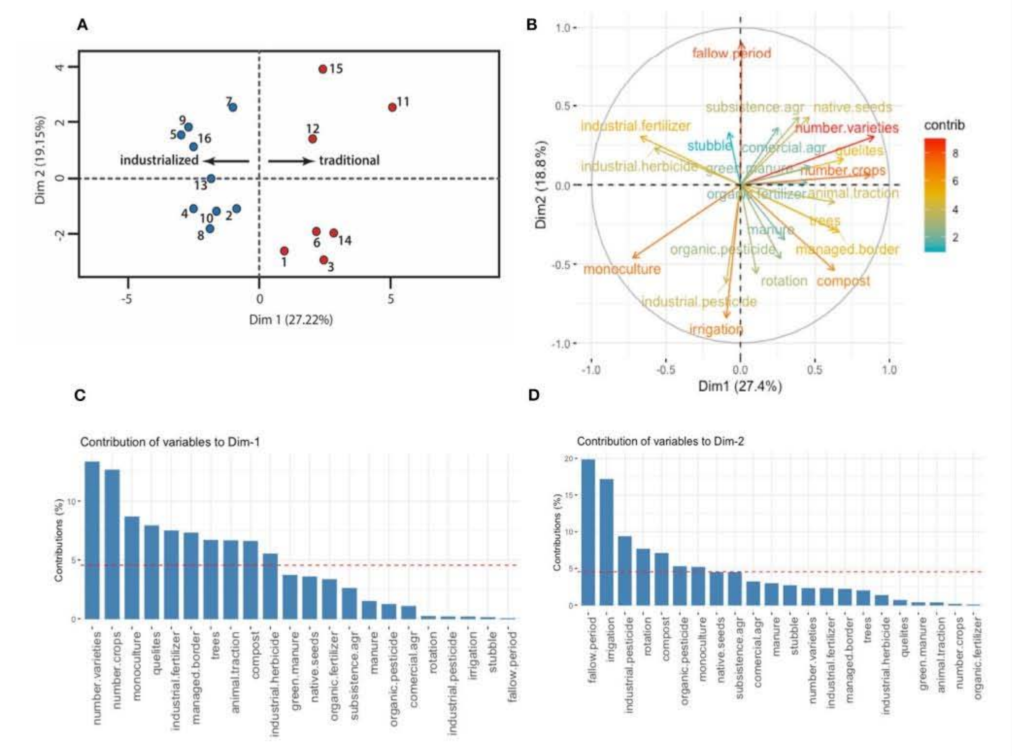

FIGURE 3 | FAMD analysis. **(A)** FAMD output for the 16 plots under study, plots on the left side correspond to the industrial management type and plots to the right correspond to the traditional management; **(B)** variables factor map, colors are given by each variable's contribution to the first and second dimensions; **(C)** contribution of variables to the first dimension; **(D)** contribution of variables to the second dimension. The reference line in **(C)** and **(D)** corresponds to the expected value if the contributions were uniform.

are frequently useful to small landholders' families in different ways), number of varieties, presence of trees and use of organic fertilizers. Likewise, there is a strong positive correlation between practices associated with an industrialized management, such as use or industrial fertilizers, herbicides and pesticides, irrigation and monoculture. We also found negative correlations (**Figure 2**, groups of red circles) between irrigation and fallow time, and subsistence agriculture and monoculture.

The FAMD we conducted explained 46.2% of the total variance in its two first dimensions (27.4 and 18.8%, respectively). **Figure 3B** corresponds to the variables factor map, where we show that the most correlated variables with the first dimension were the number of varieties within crops (0.896 correlation), number of crops (0.872 correlation), and the monoculture planting scheme (−0.722 correlation); while the second dimension was most correlated with the presence of a fallow period (0.9 correlation), irrigation (−0.84 correlation) and use of industrial pesticides (−0.62 correlation) (see **Supplementary Table 2** for a more detailed definition of each variable). Moreover, all the variables with a positive correlation to the first dimension were practices associated to a traditional management (Altieri et al., 1997): use of local seeds, crop rotation, fallow period, animal traction, presence of quelites, managed border, presence of trees, use of green manure, compost regular manure, and organic inputs. On the other hand, the variables with a negative correlation were all associated with an industrial model of agriculture (Perfecto et al., 2009): a monoculture scheme, irrigation and use of industrial inputs (fertilizers, herbicides, and pesticides).

The first dimension of the FAMD thus depicts a management gradient that goes from the most industrialized on its negative side to the most traditional on its positive side (**Figure 3A**). Based upon this result, we separated the plots falling to the right and left side of the first dimension's origin, thus discretizing the management gradient into two separate categories (industrial and traditional). By doing this, we found that 15 out of 16 plots fell in the expected side from the management category initially hypothesized by key informants. Thus, we sampled and compared coleopteran diversity among these two groups, leaving aside the one plot that did not match the original hypothesis. Note that the vertical axis was not used to further divide the plots in more groups, nevertheless it is worth saying that the variables with higher coefficients in this dimension were fallow period with a positive sign, and irrigation and pesticide use with a negative sign.

Beetle Diversity

In **Figure 4** we present an overview of the sampled diversity of families in the order Coleoptera. In total, we found 1,168 individuals belonging to 25 families, which we then identified as 80 different morphs. The most abundant families were Chrysomelidae, Cantharidae and Curculionidae, with the first two being well-represented in both management types and the last mainly in the traditional plots. We found one exclusive family to the industrialized management: Trogossitidae. Likewise, there were four families exclusively found in the traditional plots: Bostrichidae, Buprestidae, Languriidae, and Tenebrionidae.

Overall, coleopteran abundance did not show significant differences among plots from the industrialized and the traditional groups, but both family and morph richnesses were significantly higher in the traditional plots ($p = 0.0265$ and $p = 0.0203$, respectively) (**Figure 5**). **Figure 6A** depicts the results of pooling together all plots belonging to the same management category. We present morph richness inside each family in these two compound samples. Renyi diversity was higher for the traditional category, as it was significantly more diverse across all the Renyi's spectra of indexes (confidence intervals at 95%) (**Figure 6B**).

Functional groups varied strongly between management types. Traditional plots had 30% less abundance of herbivorous families, 27% more predators, 78% more detritivores, and 7% less polyphages. Herbivores were dominated by Chrysomelidae and Curculionidae; predators were mainly Cleridae, Coccinellidae and Carabidae; detritivores were dominated by Nitidulidae and Anobiidae, and polyphagues were mainly Cantharidae and Phalacridae.

The CCA showed that management variables accounted for 73% of the variance in beetle community composition, with the strongest predictor variables being: industrial herbicide, followed by industrial pesticide, quelites, industrial fertilizer, and number of crops ($p < 0.05$). **Figure 7** shows that the most correlated pairs are Curculionidae with number of crops, and Cantharidae with the use of industrial fertilizer and herbicide, while families closer to the center of the graph show weaker correlations. The most abundant predators, Cleridae, correlate the most with the presence of quelites; while the most abundant herbivores, Chrysomellidae, correlate the most with industrial herbicide and fertilizer. Nitidulidae, the most abundant detritivores, correlate better with both quelites and number of crops. The full model was statistically significant ($p < 0.001$).

Curculionidae As An Indicator of Management Type and Diversity

Curculionidae was the only family that complied with the requirements for working as an indicator: it was non-exclusive of any management type and showed a strong and different response to each one, it was also abundant and relatively easy to identify (**Figure 8A**), so we investigated its potential as an indicator of management and overall beetle diversity. The adjustment of a second degree polynomial between Cucrculionid abundance in each plot and its position along the management gradient gave a positive relation ($R = 0.50428$, $p < 0.05$), suggesting that plots with a more traditional management tend to have a higher abundance of Curculionidae (**Figure 8B**). Additionally, in **Figure 8C** we show the relation between curculionid abundance and the total richness of beetles in each plot. We first took richness at a family level but found no significant results, nevertheless, the same comparison at a morph

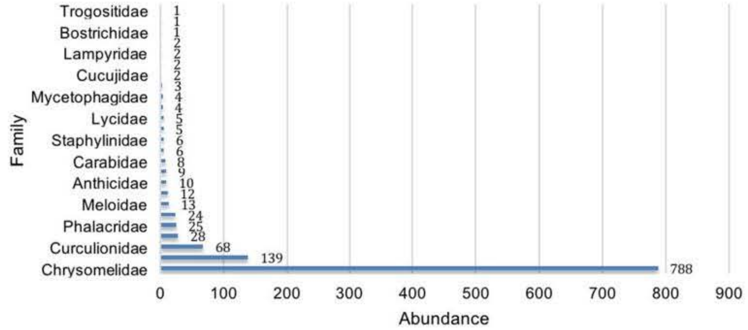

FIGURE 4 | Total abundance of every beetle family identified in the traditional and industrialized management types of maize-based agroecosystems.

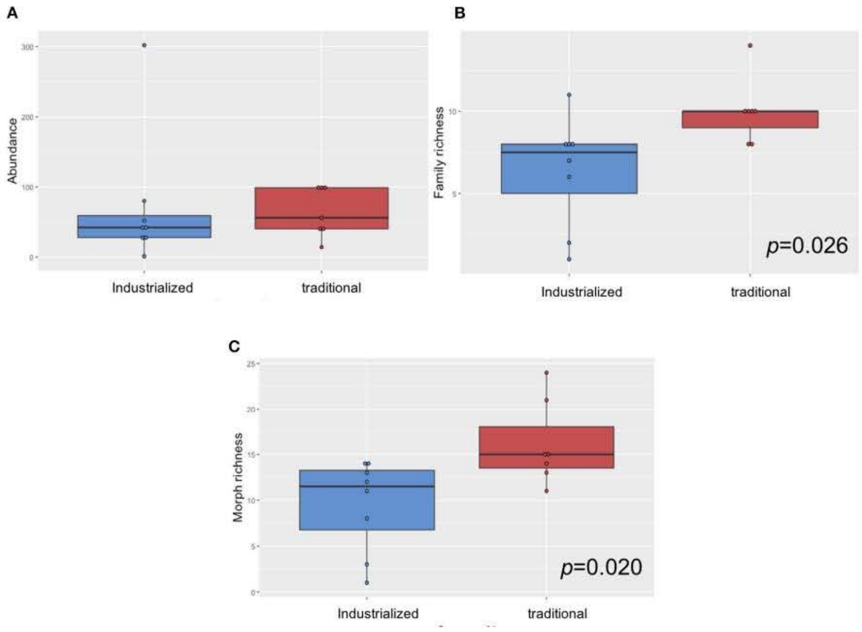

FIGURE 5 | Boxplot and ANOVA tests for **(A)** individual abundances, **(B)** family richness, and **(C)** morph richness in each management type. The median is represented by the horizontal line inside the boxes, lower and upper hinges correspond to the first and third quartiles, whiskers extend to the largest value no further than 1.5 times the interquartile range, data points are represented by circles and data beyond the whiskers are outliers. The ANOVA assumptions of equality of variances and residual normality were covered by the data: Bartlett test $p = 0.1551$ and Shapiro test $p = 0.4861$ for family richness data and Bartlett test $p = 0.6805$ and Shapiro test $p = 0.9387$ for morph richness.

level did show a significant positive relation between the two variables ($R = 0.70715$, $p < 0.05$).

DISCUSSION

In the first part of our study, we used the method by Álvarez et al. (2014) to define two broad management categories, traditional and industrialized, based upon several agricultural practices. Through the multivariate statistical approach we followed, we identified two variables to be most important for the organization of plots into these categories: total number of crops and total number of varieties grown. From an ecological point of view, crop diversity is involved in many processes both below or above ground. It is also associated with structural diversity (Del Río et al., 2003) and therefore, to the set of habitats available for the biota (feeding, refuge, reproduction spots, etc.) inhabiting or passing through the plots (Tylianakis et al., 2007; Letourneau et al., 2011; Fabian et al., 2013; Isbell et al., 2017; Liere et al., 2017). In a practical sense, this result is important given the complexity of defining different types of management in heterogeneous landscapes. Indeed, both variables can be measured with relative simplicity by academics, technicians or small landholders, and they seem to work as "umbrella" variables for many other practices associated with agricultural management, making them useful guidelines for future work that seeks to study different types of management in the region.

Another remarkable aspect is the difference in the grouping patterns of the industrialized and the traditional plots. As seen in **Figure 4**, the industrialized plots fall much closer to each other than the traditional plots. This means that even though both categories have a relatively high internal variation, the industrialized plots are far more similar to each other than the traditional ones, reflecting the tendency to homogenization that is characteristic of industrialized agriculture, in contrast with the heterogeneity and context-specificity of traditional agriculture (Gliessman, 2015). This homogenization tendency is clear, even for our study area, where the level and complexity of the machinery and inputs used in the industrialized plots is not as high as in other regions of Mexico, like El Bajio and the North of Mexico. The high variability found inside the traditional group of plots is surprising given the small scale of this work (**Figure 1**), which further illustrates the heterogeneity that can be found even in this type of landscape (Urrutia et al., 2020). This shows that the traditional management is not static or "archaic," as there is

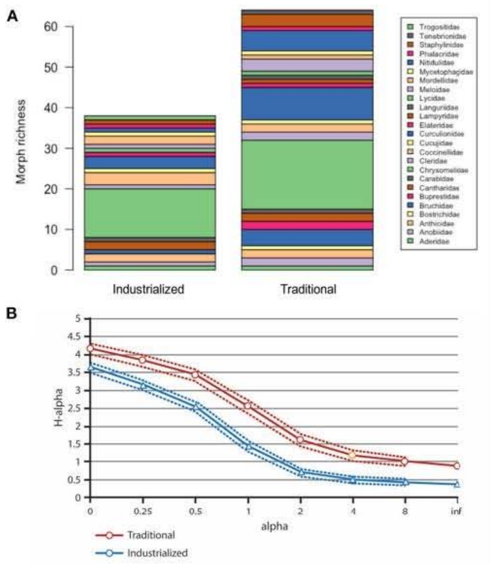

FIGURE 6 | Comparison of the industrialized vs. traditional compound samples. **(A)** Morph richness is strikingly higher for most of the families in the traditional group; **(B)** Renyi diversity is consistently higher in the traditional group.

significant variation in the practices that small landholders adopt through time and space.

As for coleopteran diversity, the traditional plots showed higher values at both family and morph level, regardless of the diversity measure used, and in spite of the fact that many of the industrialized plots were close to them (which could have otherwise brought diversity to industrialized plots). This indicates that coleopterans are significantly sensible to agricultural management even at small scales, a fact worth noting given that local communities are influenced by their surroundings and that their diversity depends on the species pool at a broad scale and on many landscape variables (Duelli et al., 1999; Gabriel et al., 2010). Moreover, management variability inside traditional and industrialized categories was also large, as we have discussed above, which makes significant inter-category differences more striking. In addition to having a higher diversity of beetles in general, the traditional plots had more exclusive species, which points to their importance as reservoirs of rare species.

In terms of trophic guilds, the traditional plots had less herbivores and more predators and detritivores, which results in a more functionally rich community with possible positive repercussions for agriculture. Namely, the bigger number of predators could be controlling the herbivorous populations and preventing potential pests, while detritivorous species could be sustaining healthier nutrient cycling processes. This may play a critical role for production, since it is estimated that 18–40% of crop losses can be attributed to herbivore arthropods (Oerke, 2006; FAO, 2017; Sharma et al., 2017), and predatory arthropods have proven important drivers of autonomous pest control mechanisms (Zhang et al., 2007; Vandermeer et al., 2010; Letourneau et al., 2011; Rusch et al., 2016). Our results are consistent with other studies that have found more natural enemies in diversified agroecosystems than in those with an industrialized management (Tooker and Frank, 2012; Torcat-Fuentes et al., 2018; Wan et al., 2019; Flores-Gutierrez et al., 2020). The reasons for this may include that natural enemies are more dependent on secondary sources of food and refuges or nesting sites, which are available in diverse environments (Bianchi et al., 2006; Chaplin-Kramer et al., 2011; Karp et al., 2018). Additionally, natural enemies appear to be more vulnerable to pesticides than herbivores, on the one hand because they too are killed by them (Theiling and Croft, 1988), but additionally, because their food sources (namely, other arthropods) are periodically depleted by pesticides while herbivores' food sources remain unaltered (Perfecto et al., 2009). The combination of predators and detritivorous beetles may be crucial in providing the ecosystemic services of pest regulation and soil fertility (Power, 2010; Tscharntke et al., 2012), which can in turn translate into a decrease in the need for agricultural inputs (Nabhan and Buchmann, 1997; Naylor and Erlich, 1997).

Moreover, the bigger amount of herbivores that we found in industrialized plots further suggests that this combination of practices is not associated to the alleviation of pest related problems. This has been documented before, with herbivore communities being sometimes unresponsive to management industrialization (Flores-Gutierrez et al., 2020) and other times being actually increased by it (Knight and Norton, 1989; Krauss et al., 2011; Meehan et al., 2011). Indeed, our CCA showed that the most abundant herbivores, the Chrysomellidae, were positively correlated to the use of industrial fertilizers and herbicides and negatively correlated to the number of crops, characteristics that together describe an industrialized management. On the other hand, the most abundant predators and detritivores, Cleridae and Nitidullidae, correlated positively with the presence of quelites and number of crops, while relating negatively to industrial inputs and irrigation, again strongly suggesting that a traditional management benefits this guild. Finally, little can be said of the polyphague guild in our analysis since it comprises families with too wide a variety of eating strategies; identification to genre or species levels would be required in order to refine the categorization of these taxa.

Regarding the family Curculionidae, we found that the abundance of this family increases as management tends to be more traditional and that it also reflects the diversity of coleopterans in general. Nevertheless, this should be taken with caution because it was the case for most, but not all the sampled plots (**Figure 3**). This said, curculionids have an easily recognizable morphology (mainly because of the anterior projection in their head) and in fact it is safe to say that all small landholders in Mexico are well-familiarized with them, so they can indeed be widely used as indicators of overall

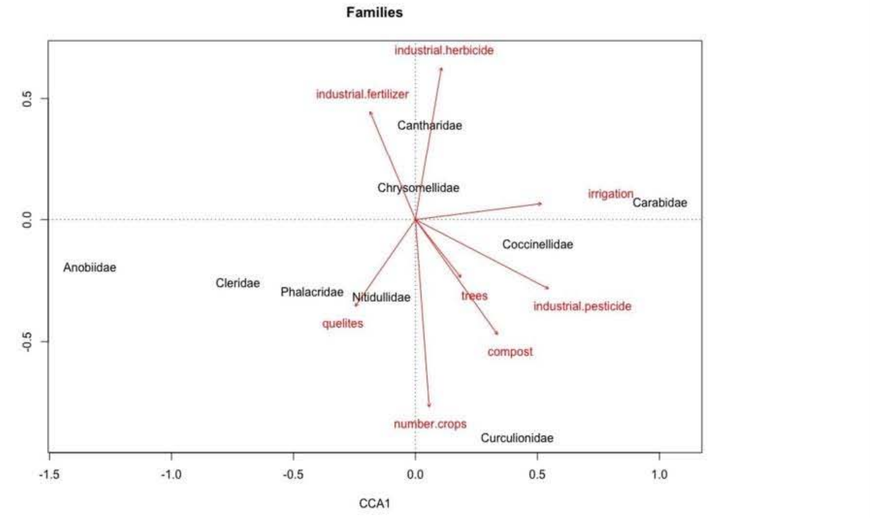

FIGURE 7 | Canonical correlation analysis of management practices and the best represented beetle families.

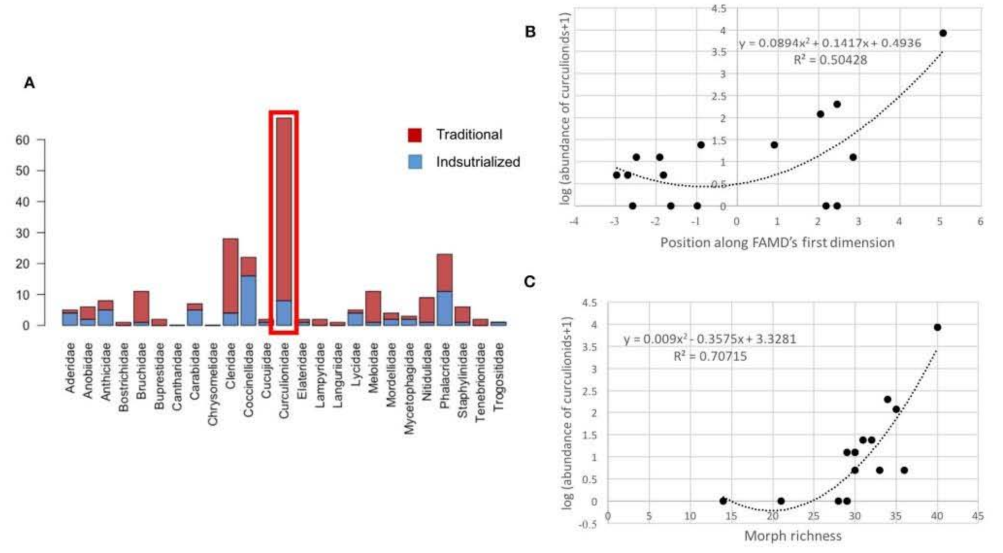

FIGURE 8 | Curculionidae as indicators of management type and coleopteran diversity. **(A)** abundance of each family in traditional and industrialized plots, **(B)** polynomial regression of curculionid abundance against management gradient, **(C)** polynomial regression of curculionid abundance against richness of beetle morphs.

coleopteran diversity or agricultural management type. The family is abundant in most of the world, and more markedly in the tropics. They mainly feed on vegetal tissue, though they can also eat lichens, algae and fungi (Morrone, 2014). According to Zimmerman (1994), all angiosperms are probably consumed by at least one curculionid species. However, they are not just herbivores, for various plants depend on curculionids for pollination (Morrone, 2014). This family has been used as an indicator of coleopteran diversity before (see Ohsawa, 2010), but we have no knowledge of it being used in Mexico or in maize-based agroecosystems. Because of its cosmopolitan nature, it would probably be found to be a good estimator of coleopteran diversity in a wide arrangement of environments. On the other hand, as an indicator of agricultural management, Silva et al. (2002) also found this family to be more diverse under a management that would fit into our traditional category.

In the agricultural context, curculionids are often thought of as a pest, because they feed on a wide range of crops (maize, beans, avocado, cotton, rice, etc.) (Morrone, 2014). However, it is worth noting that none of the small landholders interviewed in this study regarded them as an important problem (see Silva Aparicio et al., 2003 for a similar case). In general, they mentioned that curculionids bit some of the stored grains, but the amount was not considered significant and these grains were generally used to feed fowl. Also, many of them said to avoid damage by storing the grains with local herbs and flowers which repel curculionids, while only a few of the more industrialized or market-oriented producers declared the use of industrial pesticides as part of their storage practices. In any case, none of the interviewed small landholders reported significant damage by curculionids in the field.

While our work provides significant insights into the relationship between agricultural management and beetle diversity, it has limitations that should be kept in mind. We only conducted one sampling (during the rainy season), which is restricted considering the high inter-annual, inter-geographic and inter-crop variability found in coleopterans (Finn et al., 1999; Andresen, 2003). For example, in another agroecosystem, Flores-Gutierrez et al. (2020) reported that arthropod abundance of herbivores was more than 100-times greater during the rainy season than during the dry season, so our results must be taken cautiously. Also, the use of sweep nets biases samples toward foliage-dwelling insects, so it would be advisable to use other sampling techniques in further studies, as they all have shortcomings and can complement each other (Doxon et al., 2011). Our sample size was relatively small (16 plots), although the collaboration of key informants and the recollection of a large amount of beetles seemed to compensate for this, as shown by the clear differences between management types and beetle diversity (see Blanco and Castro, 2007 and Álvarez et al., 2014 for discussions on sampling for qualitative information). Given that this was a field study, we had little control over environmental variables, which made statistical replicates impossible and limited the analysis possibilities. As a counterpart, those results that were statistically significant even under the great amount of environmental noise are probably a reflection of strong tendencies.

A previous work in Zaachila, Oaxaca, has shown that patches with different land use types, such as agricultural patches, grasslands and forests, all harbor a high beetle diversity but that the species arrangement is markedly different in each of them (Ramírez-Ponce et al., 2019). In this study we were able to further differentiate agricultural land uses by organizing the large heterogeneity of management practices into two broad types. From these types, the one characterized by the use of local landraces and little external inputs harbored a larger coleopteran diversity than its more industrialized counterpart. In another work, we showed that Zaachila's landscape is characterized by a high spatial heterogeneity given by small and multiple patches, a feature that is probably shared by other areas in the tropics with similar historic and physical characteristics, and that differentiates them from the more commonly studied landscapes of the temperate regions of the world (Urrutia et al., 2020). We also showed that agricultural patches, especially rainfed-agriculture patches, dominate this rural landscape and that, given their atomized pattern and large connectivity, they play a central role in the potential migration and recolonization among the adjacent forest patches (Urrutia et al., 2020). Together, these two studies suggest that a traditional management of the agricultural patches of Zaachila contributes to a high quality matrix for biodiversity conservation. We believe that the results of this work are relevant for the conservation of biodiversity in other contexts where small landholders are still the principal actors of agriculture and where traditional practices still survive. These and other works support the key role of traditional *campesino* agriculture in the conservation of biodiversity, including agrobiodiversity and its cultural expressions in landscapes driven by small landholders (Perfecto et al., 2009; Mora Van Cauwelaert, 2017; Bellon et al., 2018), a matter that is crucial since most of the world's biodiversity lies in these regions.

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 in the article/**Supplementary Material**.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Ethics Committee of the Ecology Institute at UNAM. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

MB, LJ-B, CG and TL conceived the ideas and designed methodology. CG and TL collected the data. CG analyzed the data. CG and MB led the writing 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/fsufs.2020.590720/full#supplementary-material

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APÉNDICE VI: Combined effect of matrix quality and spatial heterogeneity on biodiversity decline

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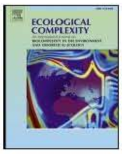

Combined effect of matrix quality and spatial heterogeneity on biodiversity decline

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ABSTRACT

The land-sparing/land-sharing debate remains an oversimplified framework to evaluate landscape management strategies that aim to reconcile food production and biodiversity conservation. Still, biodiversity-yield curves, on which the framework has relied, provide valuable qualitative information on biodiversity's sensitivity to agricultural practices, and much research has studied this relationship. But the potential effect of landscape configuration on biodiversity's response to intensification has rarely been considered; besides, studies have often taken yield as an indicator of agricultural management and have generalized conclusions from studying particular taxonomic groups. In this work we adapt a metacommunity model to analyze factors that shape biodiversity's response to agricultural intensification while addressing some of the simplifications of the sparing/sharing dichotomy. In particular, we study species richness decline in landscapes encompassing a combined gradient in matrix quality and configurational heterogeneity of habitat patches, and considering community dynamics. We found that species richness along an intensification gradient shifts from following a robust response to presenting an abrupt decline, as landscape heterogeneity increases, as minimum viable population increases or as habitat area decreases. Our work highlights the interdependent effects of heterogeneity, habitat availability and matrix quality on biodiversity and contributes to a nuanced understanding of ecological and landscape factors that enable a robust response of biodiversity in the face of spatiotemporal perturbations.

1. Introduction

In the context of global food insecurity and biodiversity loss, it is critical to develop landscape management strategies that address these interrelated problems sustainably. The land-sparing/land-sharing debate has brought attention to this issue, framing it as a dichotomy between management strategies. On one hand, land-sparing proposes to limit food production to a small surface, where high-intensity agriculture is practiced to maximize yield, while other zones are reserved for biodiversity conservation. Therefore, landscapes associated with this strategy tend to have low spatial heterogeneity and a low quality matrix, that is, habitat patches embedded in so-called intensified plots where local biodiversity is unlikely to thrive (Fischer et al., 2008; Fischer et al., 2014; Kremen, 2015). On the other hand, land-sharing proposes to use wildlife-friendly agriculture at the expense of a bigger production surface and to integrate agricultural areas with areas for conservation throughout the landscape; as a result, landscapes tend to maintain a high-quality matrix and high heterogeneity (Fischer et al., 2008; Fischer et al., 2014; Kremen, 2015). Land-sparing and land-sharing strategies can thus be thought as opposites in a combined gradient of two variables: matrix quality and spatial heterogeneity. However, most empirical and theoretical efforts to compare such strategies, including our previous work, focus on either of these variables (Villard and Metzger, 2014; Butsic and Kuemmerle, 2015; Chaplin-Kramer et al., 2015; González González et al., 2016; Liao et al., 2016); knowledge of tradeoffs and interactions encourage us to bring this a step further by explicitly considering their combined effect on biodiversity.

The land-sparing/land-sharing framework has largely relied on biodiversity-yield curves to contrast management strategies, as their shapes provide insight on the impact of agricultural practices on species persistence (Perfecto et al., 2009; Phalan et al., 2011; Butsic and

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Kuemmerle 2015; González González et al. 2016). If biodiversity declines drastically as management intensity increases, that is, following a concave up curve, then it is argued that a land-sparing approach would minimize biodiversity loss by minimizing the managed area. If, instead, biodiversity declines following a concave down curve, suggesting a robust response to low intensity agriculture, then a land-sharing approach is preferred. From a theoretical perspective, this qualitative information is valuable in evaluating biodiversity's sensitivity to agricultural intensification.

However, it is recognized that the land-sparing/land-sharing framework oversimplifies the tradeoffs involved in achieving food security and sovereignty (Chapell and LaValle, 2011; Fischer et al., 2011; Kremen, 2015; Bennett, 2017). The debate has centered on the tradeoff between yield and biodiversity conservation, often taking agricultural production as an indicator for agricultural management. For example, a common assumption is that less intense agricultural practices necessarily produce lower yields, in spite of evidence that they could satisfy global food demand (Chappell and LaValle, 2011; Tscharntke et al., 2012). Instead, it has been proposed that determining biodiversity's responses with respect to agricultural management is more pertinent in evaluating conservation strategies and in discussing food sovereignty beyond productivity (Perfecto et al., 2009; Kremen, 2015). We focus on this relationship, considering the intensification of agricultural management as the "transition from ecosystems with high planned biodiversity and a more traditional management style to low planned biodiversity and an industrial management style, such as the use of agrochemicals" (Perfecto et al., 2009:19).

Another limitation of this framework is that the spatial scale and configuration at which habitat patches should be preserved is not specified. While land-sparing strategies intend to preserve extensive and continuous habitat patches, as opposed to the small and dispersed fragments often associated with land-sharing, the heterogeneity that results from these spatial arrangements has not been defined consistently (Fischer et al., 2014; Kremen, 2015). The lack of an explicit distinction between configurational heterogeneity (spatial arrangement of cover types) and compositional heterogeneity (the number and proportions of cover types) contributes to the confusion (Fahrig et al., 2011); so, when land-sharing is said to promote higher heterogeneity than land-sparing, it is not always clear which aspect of heterogeneity it refers to. Still, in the land-sparing/land-sharing literature, configurational heterogeneity has been the most neglected, insofar as studying biodiversity's response to an intensification gradient (i.e. the reduction in the number of cover types exemplified by typical biodiversity-yield curves), accounts for the compositional aspect of heterogeneity.

The impact of configurational heterogeneity on biodiversity has mainly been studied outside the land-sparing/land-sharing framework, with an emphasis on habitat loss and fragmentation over matrix quality (Fahrig, 2003; Liao et al., 2016; Xu et al., 2018). For example, following theoretical approaches, Liao et al. (2013b) argue that the effect of spatial heterogeneity depends on dispersal type, while Laio et al. (2016) find that certain patch configurations compensate habitat loss and mitigate extinction risk. Although a few studies have taken into account both habitat quality and configuration, they do not discuss the results in the context of the land-sparing/land-sharing debate (Liao et al., 2013a, b; Wiegand et al., 2005). Here we consider the effect on biodiversity of configurational heterogeneity of habitat patches together with an intensification gradient (Fig. 1).

Finally, another limitation that concerns us is the lack of attention to community interactions when assessing biodiversity's response to intensification. Comparisons of land-sparing/land-sharing strategies in empirical studies tend to focus on particular taxonomic groups or populations instead of ecological communities (Prevedello and Vieira, 2010; Phalan et al., 2011), certainly due to the experimental challenges it implies. However, theoretical studies that account for these interactions are also scarce because most fall outside the land-sparing/land-sharing debate (see for example, Liao et al., 2016). We consider community dynamics given its potential relevance for species persistence.

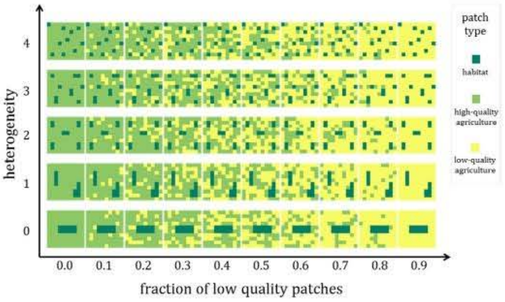

Fig. 1. Combined gradient in matrix quality and heterogeneity
Hypothetical landscapes with 10% habitat area, in a combined gradient of matrix quality (as measured by the fraction of low-quality patches in the *x*-axis) and spatial heterogeneity (as measured by total habitat edge in the *y*-axis).

In a previous work, González González and collaborators (2016) developed a spatially explicit metacommunity model to study the impact of matrix quality on biodiversity. They found that richness declines following a concave down curve as matrix quality decreases, suggesting a robust response of biodiversity to agricultural intensification; however, the study did not consider the potential effect of different landscape configurations, among other factors that may shape biodiversity-loss curves. Here we adapt this model to study the shape of richness decline in a combined gradient of matrix quality and spatial heterogeneity, and we test the effect of habitat proportion and minimum viable population on the curves' shapes. We found that as particular stresses on biodiversity increase (fragmentation, habitat loss and population vulnerability), richness decline along an intensification gradient shifts from a concave down to a concave up shape, that is, from a robust response to an abrupt decline.

2. Methods

We adapt a metacommunity model (González González et al. 2016) to study the combined effect of matrix quality and heterogeneity on biodiversity, as well as the impact of habitat proportion and minimum viable population. This model simulates the spatial distribution of a hypothetical ecological community in an agricultural landscape by coupling a local community network dynamic with a migration dynamic. We present an overview of the model and the adaptations we implemented.

2.1. Communities

Using the niche model of food webs (Williams and Martinez, 2000), we generated 100 networks of 10 trophic species. From these we built interaction matrices by assigning random weights to edges and set up a Lotka-Volterra system with which we model species interactions. For each community, the system has the form

$$\frac{dx_i}{dt} = x_i r_i + \sum_j A_{ij} x_i x_j, \tag{1}$$

where x_i is the abundance of species i, r_i is the intrinsic growth rate of species i, and A_{ij} is the interaction matrix derived from the niche model. We parameterized the system choosing random initial abundances and growth rates. Although these communities are a subset from those used in our previous work (González González et al. 2016), we adjusted parameters to achieve higher average coexistence; this allows us to measure a wider range in species richness.

2.2. Landscape

We simulate landscapes with a lattice of 10 by 10 cells with periodic boundary. Each cell represents one patch of either primary vegetation (or *habitat*), *high-quality agriculture* or *low-quality agriculture*, and may be occupied by a community, that is, interacting populations of multiple species. We define the *quality of the matrix* as the proportion of high-quality agriculture patches; thus replacing high-quality agriculture patches with low-quality ones models a decrease in matrix quality or *intensification.*

In addition, we define *landscape heterogeneity* as the total edge between habitat patches and high-quality or low-quality agriculture patches (See vertical axis on Fig. 1). We map this metric to five qualitative heterogeneity levels to ensure comparability between landscapes with different habitat area, so that for a given amount of habitat we consider the lowest possible heterogeneity (when all habitat patches are clustered and contiguous) as level 0 and the highest possible heterogeneity (when habitat patches are apart and distributed throughout the landscape) as level 4.

In our experiments we simulate biodiversity distribution in landscapes along ten degrees of intensification and five levels of heterogeneity (Fig. 1). To generate these landscapes we specified the location of habitat patches, verifying that they were sparsely distributed, and chose random positions for the other two types of patches.

2.3. Simulation

The model takes as entries a community (characterized by its interaction matrix, species' intrinsic growth rates and initial abundances) and a landscape. On initialization, only habitat patches are occupied by a community, with specified initial abundances. The model iterates between community dynamics and migration until arriving to a steady state, for which we found 100 time steps are sufficient (Fig. 2).

During each time step: i) Communities in habitat patches interact as described by the previous Lotka-Volterra system (Eq. (1)). Then, ii) a proportion of each population, in all patches, migrates to the eight neighboring patches depending on the type of patch: 30% in habitat patches and 100% in high-quality or low-quality agriculture patches; next, in all patches, a proportion of incoming populations dies as a cost of migration, again, depending on the type of patch: 0% in habitat patches, 30% in high-quality agriculture and 85% in low-quality agriculture. Coupling community and migration dynamics requires a given number *n* of migration substeps for every community dynamics substep, as these processes occur at different time scales; in our simulations $n = 5$.

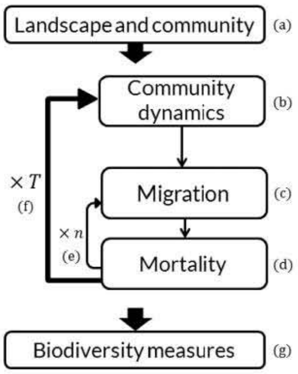

Fig. 2. Model diagram
Diagram of the implemented metacommunity model (adapted from González González et al. 2016. The model takes as entries a landscape and an ecological community (a); it iterates between a community dynamic (b) modeled as a generalized Lotka-Volterra system and a migration dynamic (c) that includes a mortality substep (d). Coupling both dynamics requires n substeps of migration and mortality for every community dynamic substep (e); we use $n = 5$. The simulation lasts T time steps until arriving to a steady state (f); we use $T = 100$. Richness is calculated from the resulting spatial distribution of species across the landscape (g).

The model's output is the spatial distribution of species across the landscape in steady state, to which we can apply richness or abundance measures. Here we focus on species richness, defined as the number of species whose final abundance in the landscape is larger than an arbitrary threshold. We interpret this parameter as the *minimum viable population*, which is the smallest isolated population with a chance of surviving despite potential demographic, environmental or genetic stochasticity (Shaffer, 1981).

2.4. Experiments and statistical analyses

We simulate biodiversity distribution in landscapes with 10% and 30% of habitat patches, and in each case we consider five heterogeneity levels and ten degrees of intensification, for a total of 50 landscapes per habitat area (Fig. 1). We run the model in every landscape with 100 hypothetical communities and measure the resulting species richness. Given that mean abundance varies by orders of magnitude among communities, we restrict the analyses to communities that can be compared under the same minimum viable population. Specifically, we select 79 communities that, at an intermediate heterogeneity level in 10%-habitat landscapes, show a change in richness along the intensification gradient under a *minimum viable population* = 30. At every combination of habitat area, heterogeneity and intensification, we calculate mean species richness and standard deviation, then we study the shape of mean richness decline as matrix quality decreases in each heterogeneity level and the differences in richness between heterogeneity levels.

In particular, at each heterogeneity level we fit first and second degree polynomials to mean species richness along the intensification gradient using the least-squares method weighted by the inverse of standard deviations and choose the best fit as the one with higher adjusted R^2. In the case of second degree polynomials, we characterize the shape of the curves by their quadratic term coefficient: a negative coefficient indicates that biodiversity decreases as a concave down curve, while a positive coefficient indicates it decreases as a concave up curve (González González et al. 2016). We then compute 95% confidence intervals by bootstraping and identify differences in richness between heterogeneity levels.

2.5. Implementation

The model, simulations, data analyses and figure creation were implemented in the Python programming language, using the libraries NumPy, SciPy, Matplotlib and Seaborn. The scripts are available in a version-control repository at [https://github.com/laparcela/MatrizAgroecologica].

3. Results

3.1. Effect of heterogeneity on the shape of richness decline curves

For each heterogeneity level in 10%-habitat landscapes (Fig. 3, Supplementary Fig. 1), we first determine whether richness declines linearly or nonlinearly. Here we use *minimum viable population* = 30. In landscapes with the lowest heterogeneity (level 0), richness declines as a concave down curve as matrix quality decreases. Next, in heterogeneity level 1, richness declines linearly with a relatively mild slope. Last, in high heterogeneity landscapes (levels 2, 3 and 4), richness

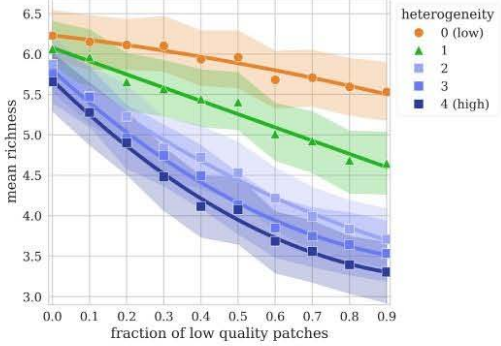

Fig. 3. Richness decline along an intensification gradient (*x*-axis) in 10%-habitat landscapes (*minimum viable population* = 30). In low heterogeneity landscapes (level 0), richness declines as a concave down curve, suggesting a robust response of biodiversity to intensification; in contrast, richness follows a concave up curve in high heterogeneity landscapes (levels 4, 3, and 2). Each data point is the average richness of 79 communities; see Supplementary Fig. 1 for full distributions. (For interpretation of the references to color in this text legend, the reader is referred to the web version of this article.)

declines as a concave up curve. This suggests that richness decline along an intensification gradient shifts from a concave down to a concave up shape as landscape heterogeneity increases.

3.2. Differences in richness between heterogeneity levels

As matrix quality decreases, richness remains higher in low heterogeneity landscapes than in high heterogeneity landscapes, but at low intensification heterogeneity does not have a considerable impact on richness. High heterogeneity landscapes have similar richness at each degree of intensification (blue curves in Fig. 3), that is, there was no statistical difference between the distribution of species richness in landscapes with heterogeneity levels 4, 3 and 2. However, along the intensification gradient landscapes at the two extremes of heterogeneity have contrasting richness. There was a significant difference in the distribution of richness between landscapes with the highest and lowest heterogeneity, that is, level 4 compared with level 0, except at 0% and 10% of intensification.

Finally, we determined where along the gradient there are three statistically distinct responses to heterogeneity levels (Fig. 4a). We compared richness distribution between (i) heterogeneity levels 4 and 1, and (ii) heterogeneity levels 1 and 0, and found significant differences in both comparisons from 70% to 90% of intensification. Thus, within that interval, richness distributions in landscapes with heterogeneity levels 4, 1 and 0 (blue, green and orange curves, respectively) are distinguishable from each other.

In order to illustrate how the matrix facilitates or restricts a metacommunity dynamic through migration, we plotted the typical spatial distribution of richness in 10%-habitat landscapes reached by a single community in our experiments (using *minimum viable population* = 0.1 for each patch), (Fig. 5). At low intensification, richness is almost uniformly distributed across the landscapes, suggesting that habitat patches are coupled in a metacommunity dynamic. In contrast, at high intensification, habitat patches become isolated, although species survive inside them (see discussion on heterogeneity).

3.3. Effect of minimum viable population on the shape of richness decline curves

We analyzed the data for high heterogeneity (level 2) varying the

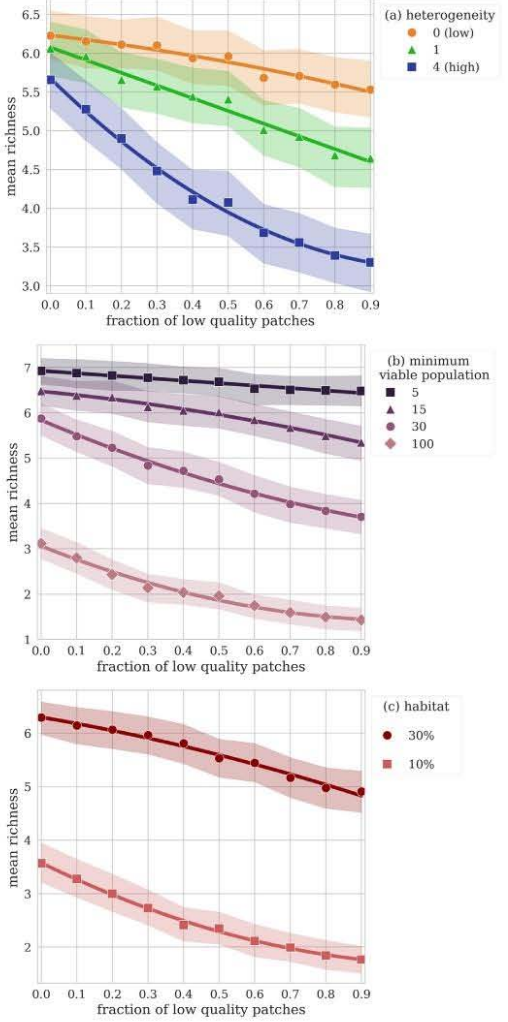

Fig. 4. Factors that shape biodiversity decline along an intensification gradient Richness decline along an intensification gradient shifts from a concave down to a concave up shape as stresses on biodiversity increase, either by (a) augmenting landscape heterogeneity, (b) increasing minimum viable population thresholds or (c) reducing habitat area. Each data point is the average richness of 79 communities.

minimum viable population in the hypothetical communities by increasing orders of magnitude ranging from 0.0001 to 100, with a detailed analysis in the interval from 1 to 100 (Fig. 4b). Below *minimum viable population* = 10 there is not a substantial loss in richness, and it generally follows a linear decline with a slight slope. Next, within the interval *minimum viable population* = 10 to *minimum viable population* = 25, richness curves gradually shift from a concave down to a concave up shape. Above *minimum viable population* = 25, richness curves consistently show a concave up curve, but at the same time the proportion of communities that are extinct on initial conditions

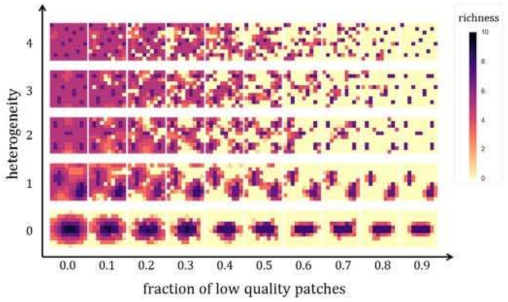

Fig. 5. Spatial distribution of richness
Typical spatial distribution of richness in 10%-habitat landscapes reached by a single community in our experiments (*minimum viable population* = 0.1 for each patch). The matrix facilitates or restricts a metacommunity dynamic: at low intensification, richness is almost uniformly distributed across the landscapes, suggesting that habitat patches are coupled in a metacommunity dynamic; in contrast, at high intensification, patches become isolated, thus increasing biodiversity's vulnerability to potential perturbations. See Supplementary Fig. 4 for scenario with 30% habitat.

increases. These trends are similar for other heterogeneity levels, though the specific threshold values where the shifts occur differ.

3.4. *Effect of habitat proportion on the shape of richness decline curves*

Although our focus is not on habitat loss per se, we repeated the previous analyses for a scenario where landscapes have 30% of habitat patches (Supplementary Fig. 2), to explore the compound effect of habitat area and intensification. Here we use *minimum viable population* = 80. In low heterogeneity levels (levels 0 and 1), richness declines linearly, although the change is small. Then, in heterogeneity levels 2 and 3, richness declines as a concave down curve; in heterogeneity level 4, richness declines linearly, but there is not a significant difference in richness distributions between levels 2, 3 and 4 at either degree of intensification. Moreover, there is not a significant difference between heterogeneity levels below 70% of intensification, and above 70% of intensification there are two statistically distinct richness distributions associated to high (levels 4, 3 and 2) and low (levels 1 and 0) heterogeneity levels, which contrasts with the three distinct responses found for 10%-habitat landscapes. While the effect of habitat proportion can be clearly observed considering a *minimum viable population* = 80, the trends mentioned above do not depend on this particular value.

Comparing richness response at the same heterogeneity level highlights the effect of habitat area on the curve shape. We consider, for example, richness decline at heterogeneity level 2 in both 10% and 30% habitat areas (Fig. 4c): in contrast with 10%-habitat landscapes, richness is notably higher in 30%-habitat landscapes and declines as a concave down curve as matrix quality decreases. Again, this suggests that a shift in the concavity of richness decline can occur as a result of reducing habitat area.

Overall, our results show that richness decline along an intensification gradient shifts from a concave down to a concave up shape as stresses on biodiversity increase, either by augmenting landscape heterogeneity (specifically, configurational heterogeneity measured as total habitat edge), increasing the threshold for minimum viable population or reducing habitat area.

4. Discussion

In this work we analyzed factors that shape biodiversity's response to agricultural intensification. We found that richness decline along an intensification gradient shifts from a concave down to a concave up curve, this is, from a more robust to a less robust biodiversity response, as landscape heterogeneity increases, as minimum viable population increases or as habitat area decreases. Our work addresses some of the simplifications that make the land-sparing/land-sharing dichotomy a limited framework for comparing landscape management strategies. In particular, we studied species richness in response to the intensification of agricultural management, rather than yield, considering both the dynamics of ecological communities and landscapes explicitly defined in a combined gradient in matrix quality and configurational heterogeneity of habitat patches.

4.1. *Heterogeneity*

Our results suggest that in landscapes with a small amount of habitat (10%), biodiversity is robust to agricultural intensification when habitat presents low heterogeneity (i.e. patches are clustered and contiguous instead of dispersed). In contrast, there is a significant impact of intensification on biodiversity in high heterogeneity landscapes, hence they also present less richness than low heterogeneity ones. The effect of heterogeneity on biodiversity becomes important as intensification increases: biodiversity is similar in landscapes with highest matrix quality, irrespective of habitat configuration, but at higher degrees of intensification, there are distinct responses of biodiversity to high and low heterogeneity. In our model, this negative effect of heterogeneity on biodiversity is due to species spending a larger amount of time in the matrix, which increases overall mortality rate.

Chaplin-Kramer et al. (2015) report a similar shift in the concavity of biodiversity response to agricultural expansion induced by forest fragmentation in realistic landscapes. They found that while mean species abundance is robust when agricultural expansion advances from forest edge in (low fragmentation), it declines rapidly in a scenario of maximal forest fragmentation. Although the focus is on habitat loss rather than intensification, these distinct responses to spatial patterns of habitat are qualitatively consistent with our results.

While in this work we consider identical dispersal rates for all species, in a theoretical study that took into account both species' dispersal abilities and landscapes with varying habitat quality comparable to the decrease in matrix quality in our model, the authors also found a negative effect of fragmentation on population size (Wiegand et al., 2005). Furthermore, in scenarios where species presented a metapopulation dynamic, fragmentation did not have an effect on population size in functionally connected landscapes (high quality matrix), but it had a large impact in landscapes with low quality matrix. This agrees with our results in that the effect of heterogeneity on biodiversity becomes more important as intensification increases.

Our results might overestimate the robustness of biodiversity's response to intensification in low heterogeneity landscapes. We expect that in these landscapes the isolation of habitat patches at high degrees of intensification (Fig. 5) would increase biodiversity's vulnerability if we introduced a local extinction probability (for example, as a function of patch size, like it is assumed in classical metapopulation models); then, despite supporting greater richness, a potential perturbation could lead to local extinctions without the possibility of recolonization from other patches. In a similar way, Kremen (2015) suggested that empirical studies favoring land-sparing might also overestimate biodiversity persistence since their limited temporal scale ignores time lags for species extinctions that result from the isolation of habitat patches in low-quality matrices. Omitting local extinction probabilities allows us to focus on the effect of fragmentation and matrix quality on biodiversity decline, though it remains an important simplification in our model.

4.2. *Minimum viable population*

We found that increasing the threshold for minimum viable population gradually turns biodiversity response to intensification from a robust response to an abrupt decline. Because population persistence depends to some extent on population size (Shaffer, 1981), it is reasonable to expect that imposing stricter conditions for species' survival (i. e. increasing the minimum viable population) generates the qualitatively different responses of biodiversity to intensification we found. Our results suggest that the range of values for the minimum viable population where biodiversity presents a robust response to intensification is smaller than that of an abrupt decline. Nevertheless, further analysis would require setting species-specific minimum viable population thresholds to reflect that they highly depend on species attributes and environmental conditions. See Larsen and Noack (2017) for an example where responses to agricultural practices depend more on individual attributes (of both crops and pests) than on landscape characteristics.

4.3. Habitat

We found that reducing habitat area (from 30% to 10%) amplifies the impact of intensification on biodiversity. Here we only considered landscapes with low levels of habitat amount, where it has been suggested that the effect of extinction threshold from habitat loss might be stronger (Fahrig, 2003). Landscapes with 10%-habitat area presented not only less richness than landscapes with the higher proportion of habitat, but a tendency towards abrupt biodiversity decline in response to intensification that contrasts with the robust response found for 30%-habitat landscapes (Fig. 4c). In our model, the negative effect of habitat loss on biodiversity is mainly due to the obvious reduction in suitable area for species' reproduction, which is a well-known cause of biodiversity decline (MacArthur and Wilson, 2015). Another, indirect, effect of habitat loss, especially in high heterogeneity landscapes, is the increased distance between habitat patches that, similarly to fragmentation, affects the time spent in the matrix, and thus, overall mortality rate.

In agreement with our results, Batáry et al. (2011) found that the effect of landscape quality is stronger in scenarios with less natural habitat. In addition, the authors highlight the role of species' dispersal rates in determining the effective distance between patches. Species with high dispersal rates are less affected by matrix quality, for instance, the high mobility of birds allows them to locate and exploit fields of high resource, independent of landscape features (Tscharntke et al., 2005; Batáry et al., 2011). On the other hand, species with low dispersal rates spend more time in between habitat patches, making them susceptible to changes in agricultural management (Thomas, 2000). Therefore dispersal rates contribute to the effect of both habitat area and heterogeneity.

4.4. Limitations

As mentioned above, considering equal minimum viable population thresholds, as well as the same preferential habitat and dispersal rates for all species is a limitation in our model. This, in turn, is a consequence of not assigning specific identities to hypothetical species. Choosing these parameters according to species' traits would make populations differentially vulnerable to intensification and other perturbations, but we cannot extrapolate from our results how it would affect community and migration dynamics. Nonetheless, the lack of information for calibrating a model with information for specific communities and landscapes makes these assumptions parsimonious (González González et al. 2016. Besides, they allow us to emphasize the general effects of matrix quality and heterogeneity over those of species' traits.

In order to relax some of the model assumptions and validate the model, future work could focus on pursuing empirical evidence for particular landscapes and ecological communities, so that the model can be adapted for a case study. Regarding the model validation, another potential route is to characterize landscape heterogeneity in sites where previous studies have empirically quantified biodiversity in different intensification scenarios. In principle, this would allow to locate previously reported results in our gradient of hypothetical landscapes and to contrast empirical evidence with our results.

5. Concluding remarks

At first sight, our results interpreted from the land-sparing/land-sharing framework would imply that land-sparing is preferable in high-heterogeneity landscapes with very little habitat whereas land-sharing is better in landscapes with greater habitat area. But this might be in conflict with the widespread association of land-sharing to high-heterogeneity landscapes and land-sparing to high-habitat ones. A conceptual gap in the land-sparing/land-sharing debate with respect to the characterization of landscape heterogeneity underlies this inconsistency and limits the comparison of management strategies. It has been argued that an ideal strategy would combine features of both sharing and sparing (Butsic and Kuemmerle, 2015; Kremen, 2015); however, locating management strategies within a continuum requires, in the first place, defining such continuum in the variables of interest.

We expect that our findings and the proposed model contribute to a nuanced understanding of how different landscape and ecological factors shape biodiversity response to agricultural intensification. In particular, our work illustrates the interdependent effects of heterogeneity, habitat availability and matrix quality, which could inform the design of management strategies. If a given strategy was preferred, but it imposed constraints on landscape composition or configuration, then our theoretical approach could help explore complementary landscape components that could be managed to support a robust biodiversity response. For example, beyond the land-sharing/land-sparing debate, it has been argued that small-scale agroecological strategies are key to achieve food sovereignty, which considers the preservation of biocultural heritage, high-quality soil and clean water availability, low-input food production and distribution, and the associated human rights to health, adequate and safe food, land and cultural identity (De Schutter, 2010; Chappell et al., 2013; Holt-Giménez and Altieri, 2013; Benett, 2017; González-Ortega et al., 2017). If such small-scale agroecological strategies were favored, one could ask what landscape elements could be managed to balance conservation and production goals under this scenario. Thus, rather than recommending general guidelines, our work provides tools for the discussion of integrative and sustainable management strategies.

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Declarations of interests

None.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecocom.2018.10.001.

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APÉNDICE VII: Landscape heterogeneity of peasant-managed agricultural matrices

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Landscape heterogeneity of peasant-managed agricultural matrices

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A B S T R A C T

Management practices, environmental and social factors shape complex agricultural landscapes. In turn, the structure of such landscapes impacts biodiversity conservation, for instance, by mediating wildlife migration between agricultural and habitat patches and thus determining the persistence of metapopulations. Landscape ecology has used heterogeneity metrics and has systematically examined how they change with grain size and landscape extent to formally characterize a landscape, its structure and potential role in the persistence of wild metapopulations. These metrics provide valuable information regarding the landscape connectivity, patch diversity and shape. However, heterogeneity metrics have rarely been applied to tropical or subtropical, peasant-managed landscapes, even though this type of landscape occupies most of the agricultural surface in or near biodiversity hotspots. We focus on a peasant-managed agricultural landscape in Oaxaca, Mexico. For this landscape we mapped and quantified the land-use classes (48 % for agricultural land use, with *kappa* = 88.85 %). We also calculated heterogeneity metrics and examined their response to changes in grain and extent scales. This allowed us to further understand the structure and conservation potential of the agricultural matrix in this type of landscape, in comparison with other agricultural landscapes in Eastern North America. Our results also enabled us to recommend specific landscape metrics such as Largest Patch Index, Shape Index, and Interspersion & Juxtaposition Index, for different types of studies involving the link between agricultural matrices and conservation. We conclude that this type of agricultural matrix is ideal to pursue joint agricultural and conservation strategies in an integrated landscape.

1. Introduction

Biodiversity conservation research at the landscape scale has mainly focused on the characteristics of habitat patches (primary vegetation). Nevertheless, attention to the anthropogenic matrix surrounding the habitat has increased in recent years (Fahrig et al., 2011; Franklin and Lindenmayer, 2009; Perfecto et al., 2009). Several studies have shown that this matrix has a great impact on species persistence, preventing or allowing migration and re-colonization amongst habitat patches in the landscape, thus promoting or preventing regional extinctions (Dunning et al., 1992; Franklin and Lindenmayer, 2009; Levins, 1969; Perfecto et al., 2009; Tscharntke et al., 2012). It is also known that matrices are not homogeneous nor are they equally beneficial for the persistence of all species. The quality of a matrix, understood as its permeability for the transit of local biodiversity, varies largely depending on its spatial structure and on the type of human activities that are performed in it (Fahrig et al., 2011; Perfecto et al., 2009; Tscharntke et al., 2012; Vandermeer and Perfecto, 2007). For instance, a matrix with a structure such that connectivity among classes of land use and vegetation is large may promote biodiversity transit and, in turn, persistence at the landscape scale (Perfecto and Vandermeer, 2010; Ramos et al., 2018).

To fully understand the quality of a matrix in terms of is potential for conservation, a formal landscape perspective is needed. Landscape ecology, through the study of landscape heterogeneity, has been characterizing the effects of spatial patterns in ecological processes for more than thirty years (Burel, 1989; Gökyer, 2013; Levin, 1992; Wu, 2004; Wu et al., 2002). Spatial heterogeneity is divided into compositional heterogeneity, which refers to the number and types of patches that constitute a landscape, and configurational heterogeneity, which corresponds to the arrangement of these patches in the landscape, how

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fragmented the landscape is, the density of its borders and the connectivity among classes of patches, among other features (Fahrig et al., 2011; Wu, 2004; Wu et al., 2002). All of these attributes partially determine the quality of a matrix, as they define how accessible different resources for biological populations in a landscape are and how reachable are habitat patches for wild metapopulations (Jaeger, 2014; Reis Madeiros et al., 2019; Thies and Tscharntke, 1999; Tscharntke et al., 2012). Even though there are well established metrics to assess such landscape features (Cushman et al., 2008; Mcgarigal, 2001), their potential to inform on conservation issues in agricultural landscapes has not been fully exploited, especially outside temperate regions.

Currently, most of the world's habitat matrix composition is agricultural (Fahrig et al., 2011; Foley, 2005; Kremen, 2015). This highlights the central role of agricultural practices and their distribution in a landscape on biodiversity conservation. Indeed, depending on its composition and configuration, the agricultural matrix can act as a refuge for biodiversity, as a facilitator for the movement of organisms among habitat patches, and may thus help maintaining metapopulation dynamics and long-term survival of wild species (Philpott et al., 2008; Vandermeer and Carvajal, 2001; Vandermeer and Perfecto, 2007). As a result, the role of the agricultural matrix on biodiversity conservation largely depends on the type of practices and spatial organization of agriculture and other land-use classes in the matrix (González González et al., 2016; Ramos et al., 2018).

In order to understand the effects of agricultural management on biodiversity, landscape metrics provide a formal way to measure the spatial characteristics of the matrices under study. Since management strategies alter both the composition and configuration of matrices, we expect that contrasting types of agricultural practices and management and land ownership histories will show differences in landscape heterogeneity metrics. In turn, matrices of higher heterogeneity, have been regarded as more suitable for biodiversity conservation. It has been suggested, for instance, that highly heterogeneous landscapes dominated by small-scale or peasant agriculture are linked with higher permeability for biodiversity, and are thus more suited for integrated, rather than separated, production and conservation areas (Fahrig et al., 2011; Kremen, 2015; Perfecto et al., 2009). Designing optimal conservation and production schemes, and overcoming stagnated debates (e.g. land-sharing/land-sparing; Bennet, 2017; Kremen, 2015; Ortega-Álvarez et al., 2018), require spatial characterization of landscapes.

In order to properly spatially characterize an agricultural matrix, we need to consider some scale issues. Ecological patterns and processes that matter at a certain scale may not be relevant at another one or may be extremely scale-specific. For this reason, a great deal of information can be lost when delimiting a particular spatial area (extent) and a particular grain size to study a landscape. These scale-related issues have been studied for decades as part of the modifiable areal unit problem, and they have driven the sought for methods capable of preserving information across different scales or at least able to quantify the loss of information when scales change (Teng et al., 2016; Turner, 1990; Wu, 2004; Zhang and Li, 2013).

To address how landscape metrics change with grain size or extent several authors have used scalograms (Teng et al., 2016; Wu, 2004; Wu et al., 2002; Zhang and Li, 2013). Based on these graphic representations, metrics can be classified by their diverse behaviors and based on how consistent these behaviors are across landscapes, how predictable responses are to changes of scale, and whether relationships between scale and metrics can be represented with simple scaling equations or are staircase-like or erratic (Teng et al., 2016; Wu, 2004; Wu et al., 2002; Zhang and Li, 2013). The interpretation, comparison and application of landscape metrics across different conditions and with different objectives could differ markedly among scales. Thus, examining how metrics behave with scale changes is crucial. Therefore, in order to fully approach the ecological processes occurring in a landscape, it is crucial not only to calculate landscape metrics, but also to explore how landscape properties inferred through metrics change across scales (Peters et al., 2007; Wu, 2004; Wu et al., 2002).

Landscape studies examining the effect of scale have been carried out mainly in simulated landscapes or in temperate regions (Fahrig, 2003; Mcgarigal and Cushman, 2002; Shen et al., 2004), which tend to have fewer land uses and land-cover types (Brown, 2014; Gliessman, 1992) than the tropics. Given that geological, biological, and human processes that determine these landscape properties can be very different in the tropics, studies examining landscape heterogeneity metrics are urgently needed for these areas of the world. Agricultural landscapes in the tropics tend to be dominated by small plots of farms managed by peasants, and have been postulated to be relatively diverse in terms of land use class and highly connected among land-use classes (Fahrig et al., 2011). Although heterogeneity studies have been conducted in tropical areas, they have mostly focused on fragmented tropical forests (Arroyo-Rodríguez et al., 2017; Concepcion et al., 2008; Sánchez-de-Jesús et al., 2015), and have not usually considered agricultural landscapes. Considering the key role of the agricultural matrix in the conservation of tropical biodiversity (Perfecto et al., 2009), studies examining heterogeneity in tropical agricultural landscapes could guide the design of coexisting integrative productive and conservation activities.

Peasant agriculture is highly representative of agricultural practices in Mexico as it contributes with 25.5 % of national maize production and has the potential to feed half of the population (Bellon et al., 2018; CEMDA, 2017). This kind of agriculture is usually associated to a relatively fragmented and heterogeneous landscape, as most of the agricultural plots are small (< 5 ha) and very diverse in terms of management (Bellon et al., 2018; Fahrig et al., 2011). However, the formal characterization of peasant driven landscapes in the tropics remains largely unexplored.

Therefore, we focused on a peasant-driven agricultural landscape in a rural region that is in many ways similar to most of the small-scale agriculture practiced in Mexico. Our objectives were to: i) Generate a land-use and vegetation map and characterize it through landscape metrics, examining their behavior with changes in grain size (level of resolution), and extent (total studied area). In contrast to intensive agriculture in temperate regions, we expected to find a large number of patches, high patch richness and high values in connectivity and intercalation metrics. ii) Postulate specific metrics and scales that could be used in future studies aiming to characterize highly heterogeneous matrices in tropical and subtropical landscapes as the one studied here. iii) Discuss the potential of coexisting productive and conservation strategies, and practices that can potentiate these efforts.

2. Material and methods

2.1. Study site

La Villa de Zaachila, henceforth Zaachila, is a municipality in the Central Valleys of the state of Oaxaca, Mexico. It is located 17 km south of the city of Oaxaca, between 96° 40′and 96° 47′ longitude and 16° 54′and 17° 05′ latitude, and has an area of 81 km^2 at an elevation of 1500 m. Zaachila has a semi-dry-semi-warm climate, the rainy season is from June to October with an annual average temperature of 17.5 °C. The primary vegetation is deciduous lowland rainforest, along with oak-pine forest in mountain ranges in the east and west borders of the municipality (INEGI, 2010). The basement of the municipality is from the pre-Cambrian Oaxacan Complex constituted by metasedimentary rocks such as gneiss de facies and granulite marbles. To the north and west of the valley, the basement is colluvial and to the east we find sedimentary and metamorphic rocks (sandstones, shales and limestones) (Belmonte-Jiménez et al., 2005; Ortega-Gutierrez, 1981; Sedlock et al., 1993).

The known history of landscape management of Zaachila begins with the Zapotec, about 3500 years ago. Throughout its history, the municipality has had different management and land holding systems

Table 1
Landscape metrics used in this study.

Landscape metric	Abbreviation	Landscape metric	Land use Class metric	Description (McGarigal et al., 2012)
Number of Patches	NP	x	X	Number of patches in the landscape. Simpler fragmentation metric.
Patch Richness	PR	x		Number of different types of patches in the landscape. Relatively simple spatial composition metric; does not reflect the relative abundance of patch types.
Shannon's Diversity Index	SHDI	x		Metric of landscape diversity particularly sensitive to rare patch types. It is the sum for all the patches, of the proportional abundance of each type of patch multiplied by the proportion.
Largest Patch Index	LPI	x	X	Percentage of the total area that is covered by the largest fragment of a class type in the total if it is calculated at the landscape level. LPI approaches 0 when the largest fragment area of the corresponding class is very small and is equal to 100 when the landscape total consists of a single class that occupies 100 % of the landscape.
Edge Density	ED	x	X	Useful metric when comparing edge of different landscapes. Sum of the lengths of all the edge segments of the landscape, divided by the total area of the landscape, multiplied by 10000 (ha).
Shape Index Mean	SHAPE_MN	x	X	Measure that allows to understand the degree of dispersion of each patch in the landscape. It is the perimeter of the patches divided by the minimum possible perimeter for the most compact patch possible.
Interspersion and Juxtaposition Index	IJI	x	X	Metric that evaluates the adjacencies of the patches and measures the interrelation between different types of patches. It is the subtraction of the length of each type of unique edge that involves a particular type of patch, divided by the total length of the edge that involves the same type, multiplied by the logarithm of the same quantity, added with each type of unique edge divided by the logarithm of the number of patch types minus 1, multiplied by 100.
Proximity Index Mean	PROX_MN	x	X	This metric characterizes the degree of spatial isolation of the fragments, taking into account all the closest fragments that are within a specified search radius. High proximity values indicate that neighboring fragments, of the same type of coverage, are less isolated, large and aggregated. Low values indicate that the fragments are isolated and may have small sizes.
Total (Class) Area	CA		X	Area of the landscape that occupies the class or how much of the landscape is composed by a type of patch.
Percentage of Landscape	PLAND		X	Percentage occupied by one type of coverage in the total landscape. It is the most elementary metric in the study of landscape patterns. The percentage changes in time give information about the increase and decrease of the areas of a certain type of coverage. PLAND approaches 0 when the type of coverage decreases its area and approaches 100 when the landscape total dominates.

(Ruiz Medrano, 2011). Zaachila currently has a total of 17 human settlements (2 urban and 15 rural) and had 34,101 inhabitants in 2010, of which 80 % were concentrated in the two urban locations: La Villa de Zaachila and Vicente Guerrero (INEGI, 2010). The agricultural plots are mostly managed by peasants for family or local consumption (Mora Van Cauwelaert, 2016). In contrast with most agricultural sites in many other countries, a large percentage of these plots represent communal land, the so-called *ejidos* (INEGI 2010; Mora Van Cauwelaert, 2016). Historically, Zaachila has been an important point for regional commerce, as its traditional market has existed since before the fifteenth century, and even now it gathers farmers and peasants from all the surrounding villages. The village and the market are also reservoirs of great culinary diversity that is often associated with local landraces and management practices (Mora Van Cauwelaert, 2016).

2.2. Land use and vegetation map

To create the land use and vegetation map, we used a remote sensing image (Copernicus Sentinel-2 2017) from the dry season (May of 2016) and considered five land-use classes (Urban, Grassland, Rainfed agriculture, Irrigated agriculture, and Forest). Within these five land-use classes we found the diversity of managements associated with the peasant agricultural practices of the area. We selected the land-use classes based on INEGI's Series V chart of land use and vegetation use, scale 1: 250 000 with spatial resolution of 30 m (Series V, INEGI, 2013) and the NALCMS land use map made by CIEC for North America, scale 1:2500 000 with spatial resolution of 250 m (Colditz et al., 2012). The polygon delimitation corresponds to the political boundaries of the Zaachila municipality, which in turn correspond to the organization of public databases and fieldwork permits.

In order to map and verify specific land uses, we generated, through QGIS 2.18.7 (QGIS Development Team, 2017), 278 random points for Zaachila and visited them from September to October 2017. The status of the vegetation and land use classes was assessed by visual inspection with the support of local informers. We georeferenced points using the GPS map 64 of Garmin (error range ~ 3 m), with a minimum distance of 5 m between each reference point.

We performed a supervised classification with the maximum likelihood algorithm of ENVI version 4.7 (Chuvieco, 2009; Schuster et al., 2012). We based the selection of the training areas on the Normalized Vegetation Index (NDVI) and the combination of natural and infrared RGB bands. These areas included 404 training points, each one corresponding to a ROI (region of interest). 200 of these training points were obtained from those registered the field trips and 204 were obtained by manually determining their class through inspecting their band composition, two-dimensional dispersion graphics and position in the INEGI maps. We determined the accuracy of the classification with the remaining 78 validation points from the field trips. We used the confusion matrix and the Cohen's Kappa statistic to determine accuracy. We manually added the classes of water and greenhouses in QGIS 2.18.7 (QGIS Development Team, 2017), which were plotted using the INEGI topographic chart for water bodies and corroborating field trips. However, in the final heterogeneity analyses, we did not include the data of the greenhouse class due to its negligible area (0.089 %) (Series V, INEGI, 2013). In order to improve the accuracy of the map we carried out a post-classification process to reduce the so-called salt and pepper effect. To do so, we reclassified manually the classes of patches conformed of 4 or less pixels to the class of the closest patch with more than 4 pixels.

2.3. Spatial heterogeneity characterization and scalograms

We characterized the site's heterogeneity by estimating several landscape metrics. We calculated eight metrics of spatial heterogeneity for the landscape level and eight metrics for the land use class level (hereafter called class level). Six of these metrics apply to both

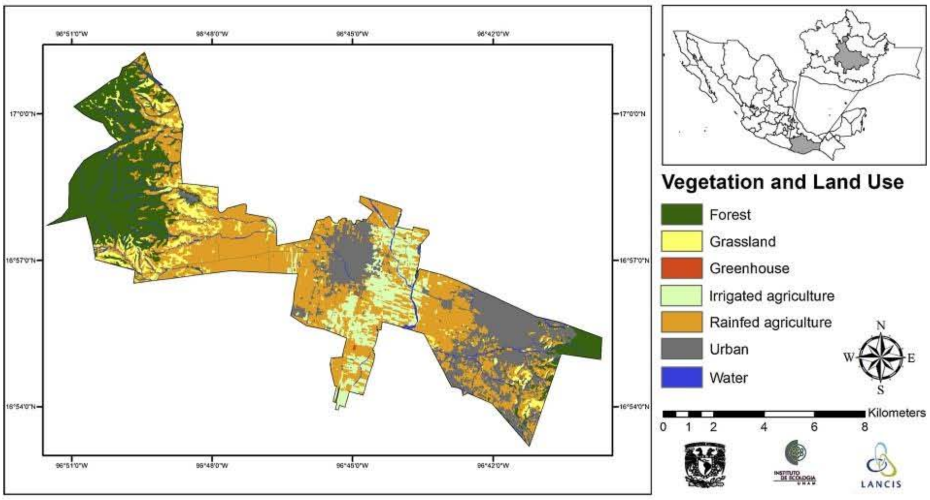

Fig. 1. Zaachila's land use and vegetation map with seven patch types, grain of 10 × 10 m and extent of 81 km2.

landscape and class level, while two are specific for landscape level (patch richness and Shannon's diversity index) and two for class level (total (area) class and percentage of landscape), for a total of ten different metrics (Table 1). We selected these metrics to include both compositional and configurational heterogeneity, and for their suitability to characterize the agricultural matrix in terms of area, density, edge, shape, isolation, proximity, interspersion and diversity (Table 1). We analyzed spatial heterogeneity using FRAGSTATS 4.2.1 (McGarigal, et al. 2012).

In order to study the effect of the spatial scale on the landscape metrics, we built scalograms that described the response of each metric to changes in extent and grain size. Scalograms show how a metric responds to scale changes, and have been widely used to study sudden shifts in curves that could suggest hierarchical occurrences or critical scales (Zhang and Li, 2013). To test the effect of change in grain size we took the initial spatial resolution of the raster, which was 10 × 10 m in a total extent of 81 km^2. The spatial resolution of the entire map was increased by 1 until it reached 100 × 100 pixels, keeping the extent constant. We assigned the grain identity resampling by majority. As for the effect of the extent, we took the complete extent of the quadrant surrounding the municipality (441 km2) and reduced it by 10 km2 until it reached 10 km2 (a similar approach to generate grain and extent scalograms was followed by Wu et al., 2002; Wu, 2004; Zhang and Li, 2013; Teng et al., 2016). Thus, we generated a total of 2000 images to represent the vegetation and land use of Zaachila.

We built scalograms plotting metric values against grain size or extent in R 3.4.3 (R Core Team, 2017). We used scalograms to: i) describe the behavior of the class level metrics, ii) classify the landscape level metric behavior in the face of scale changes, iii) test if changes in the metric with scale variation could be fitted with simple functional models, and iv) explore the sensitivity of metrics to scale change (Supplementary material Table 2–4). Besides describing the overall trends of metric behavior with grain or extent scale change, it is important to characterize their sensitivity to small changes in the scale. To that end, we employed the coefficient of variation (CV), which expresses the standard deviation as a proportion of the average metric value. We used the CV to compare variation levels across landscape metrics. The larger the CV, the higher the sensitivity of the metric to changes in scale was (Teng et al., 2016) (Supplementary Material Table 4).

To examine whether a simple model could fit to scalograms we used linear, polynomial or exponential functions and calculated residuals. Model residuals were used to visually inspect whether there were trends in the lack of fit with the change in grain size or extent (predictor variable in models) (Supplementary Material Figs. 1 and 2).

2.4. Comparisons with other agricultural landscapes

In order to test if and how different conservation/production strategies were reflected on landscape heterogeneity metrics, once landscape metrics were calculated, we compared them with those of 12 other agricultural landscapes of the METALAND database corresponding to agricultural sites in the east of the United States, all of them in the Fruitful Rim and Basin and Range USDA Farm resource regions (previously located in the Pacific USDA Farm region) (Cardille et al., 2017; USDA, 2000). METALAND includes landscape metrics previously calculated with FRAGSTATS in landscapes of 6.5 km x 6.5 km in 8 million km2 in Eastern USA. We chose 12 landscapes that had the same percentage of agricultural land use as Zaachila, had similar percentages of urban land use and primary vegetation and alike geomorphology. For it to be comparable with the Zaachila landscape, we took a fragment of the map of the municipality that had extent (6.5 km x 6.5 km) and grain size (30 × 30 m) equal to the ones obtained in METALAND. We compared most of the landscape level metrics from Zaachila with the METALAND database, with the exception of proximity index mean and patch richness, metrics that were not comparable because of the particular characteristics that have to be defined for each metric.

3. Results

3.1. Land use and vegetation characterization

The general accuracy of the land use map was 88.85 %, with a Kappa statistical index of 0.85, which is well above the minimum Kappa values required for reliable land use and vegetation maps. The class that had the highest precision values in the confusion matrix was seasonal agriculture (96.1 %), while grassland was the lowest (79.25 %). (Supplementary Material Table 1) (Congalton, 1991). The landscape of

Zaachila is mainly agricultural (48 %), being rainfed agriculture the most prevalent land use class in the municipality (39 %). The next most represented class is the secondary forest (23 %), followed by the urban zone (19 %). The classes with less coverage in the landscape are water bodies and greenhouses (Fig. 1). This makes Zaachila a predominantly rainfed agricultural landscape with few with forest remnants, useful to study the potential of an agricultural matrix connecting habitat patches (Fig. 1).

3.2. Landscape characterization

In terms of landscape level metrics, we found a very high number of patches (1867) and Shannon diversity index (1.54) (see also section below), with high dominance of forest patches in terms of area (the largest forest patch occupies 13.8 % of the landscape). The edge density was 125.13 m per ha and the average shape was 1.55, which means that the patches tend to be elongated. The interspersion and juxtaposition index was 74.97 % and the average proximity index mean within an area of 400 m was 1140, describing an intricate array of patches with a relatively high connectivity among them (Supplementary Material Table 5).

Regarding the class level metrics, the rainfed agriculture patches had the largest edge density (85.57 m/ha) and the highest interspersion and juxtaposition index (88.31 %), which means that this patch type is the most connected with other patch types, even if the largest patch in the landscape is a forest patch. However, the patch type with the highest proximity index mean (2961.07) was urban, which means that urban patches are the less isolated (Supplementary Material Table 6).

3.3. Response of metrics to changing scale at the landscape level

We plotted scalograms for the metrics in Table 1 and classified their behavior following Wu et al. (2002), (2004) and Teng et al. (2016) into four types: 1) consistent scaling relation (adjusted to a linear, polynomial or exponential function), 2) staircase-like response 3) invariant or non-answering to scale change and 4) erratic response (Fig. 2, Table 2 and Supplementary Material Fig. 1). In most cases, data violated homoscedasticity assumptions, so fits were only used for visual inspection of trends (Fig. 2). Type 1 scalograms were the most common and pointed to metrics that are useful to describe matrix heterogeneity, as they appear to have a predictable behavior in response to scale changes. Metrics with type 1 scalograms were number of patches, largest patch index, shape index mean and interspersion and juxtaposition index (Fig. 2 and Table 2).

3.4. Responses of metrics to changing scale at the class level

We also plotted scalograms for class level metrics (Table 1). In general, the behavior of each class level metric was different, therefore, we could not classify them as we did for landscape level metrics. The scale change of the extent had a greater effect on these metrics than the change of grain size. For Zaachila, for an extent greater than 300 km^2 we can observe a stabilization of the following metrics: total (class) area, percentage of landscape, number of patches, largest patch index, edge density and interspersion and juxtaposition index (Fig. 3B). For extent < 300 km^2, metrics had steps or non stabilized behavior. Moreover, for two metrics (number of patches and proximity index mean), there seems to be a 60 m grain size threshold above which it becomes harder to differentiate information between classes (Fig. 3A and Supplementary Material Fig. 2).

3.5. Comparison with metrics and scalograms in other agricultural systems

Compared with the values of the average metrics of twelve North American landscapes, the number of patches and the Shannon index in Zaachila were strikingly high. On the other hand, the shape index mean was visibly lower, perhaps due to the arrangement and distribution of small agricultural units into elongated plots, unlike the large land units of North American farmers (Fig. 4). It is also worth noting that the Zaachila landscape exhibits a significantly higher patch diversity (Shannon index, Fig. 4) and significantly less dominance of any class (Largest patch index, Fig. 4) than agricultural landscapes in North America.

3.6. Sensitivity of the matrix descriptors response to scale change

Sensitivity can be understood as the size of variations or fluctuations around fitted models and can be examined through residuals (when it is possible to fit a functional model) and also using the coefficient of variation (see Methods). Most of the landscape level metrics show low sensitivity for small changes in scale. Class level metrics, on the contrary, show relatively high sensitivity for small changes in scale (Supplementary material Table 4).

4. Discussion

In this work, we have characterized elements of the composition and configuration of a peasant-managed landscape in Oaxaca, Mexico, which is representative of the largely understudied but crucial agricultural landscapes of the tropics, given their role in conservation and their potential to implement joint agricultural and conservation strategies.

Overall, Zaachila's landscape is remarkably heterogeneous, as previously suggested for peasant-managed landscapes in the tropics (Fahrig et al., 2011), especially when contrasted with agricultural landscapes of comparable size, geomorphology and percentage of agriculture, in eastern North America. Specifically, while the edge density between both types of landscapes was similar, the interspersion and juxtaposition indices were higher in Zaachila (Fig. 4), revealing an intricate arrangement of patches, and suggesting that this landscape has large connectivity among patches. Also, Zaachila's landscape is associated to an agricultural matrix with high number of patches, high patch richness, small patch dominance, high Shannon index for patch diversity and high values in connectivity and intercalation metrics. While the comparison between Zaachila and Eastern North American landscapes of similar size and percentage of agricultural land is rather rough, it recovers the expected differences in most of the metrics used to characterize these landscapes and provides a more nuanced understanding of the differences in their spatial arrangements. This also validates and highlights the value of landscape metrics for the formal assessment and comparison of agricultural landscapes.

In order to further discuss the quality and potential of Zaachila's agricultural matrix in terms of biodiversity conservation, we will focus on the metrics describing the forest and rainfed agriculture classes, the two key classes in terms of strategies to articulate agricultural production and biodiversity conservation. Rainfed agriculture has a large interspersion and juxtaposition index, edge density and has little dominance (small largest patch index) (Supplementary Material Table 6). This is, rainfed agriculture is in contact with all types of patches. In contrast, the forest patch distribution is dominated by the largest patches, has little edge density and small interspersion and juxtaposition index (Supplementary Material Table 6). In other words, the forest class is concentrated in few, large patches with relatively little contact with the rest of the matrix. Considering that forest patches are in general apart from each other and that this may hinder metapopulation migration and recolonization dynamics, the matrix surrounding forest patches becomes central for the conservation of wild metapopulations. Since such matrix is dominated by rainfed agriculture, which in turn has a potentially high connectivity, it is crucial to maintain and foster agricultural practices that provide this class with a high permeability for local biodiversity (Vandermeer and Perfecto, 2007; González González, 2018). These practices include local peasant

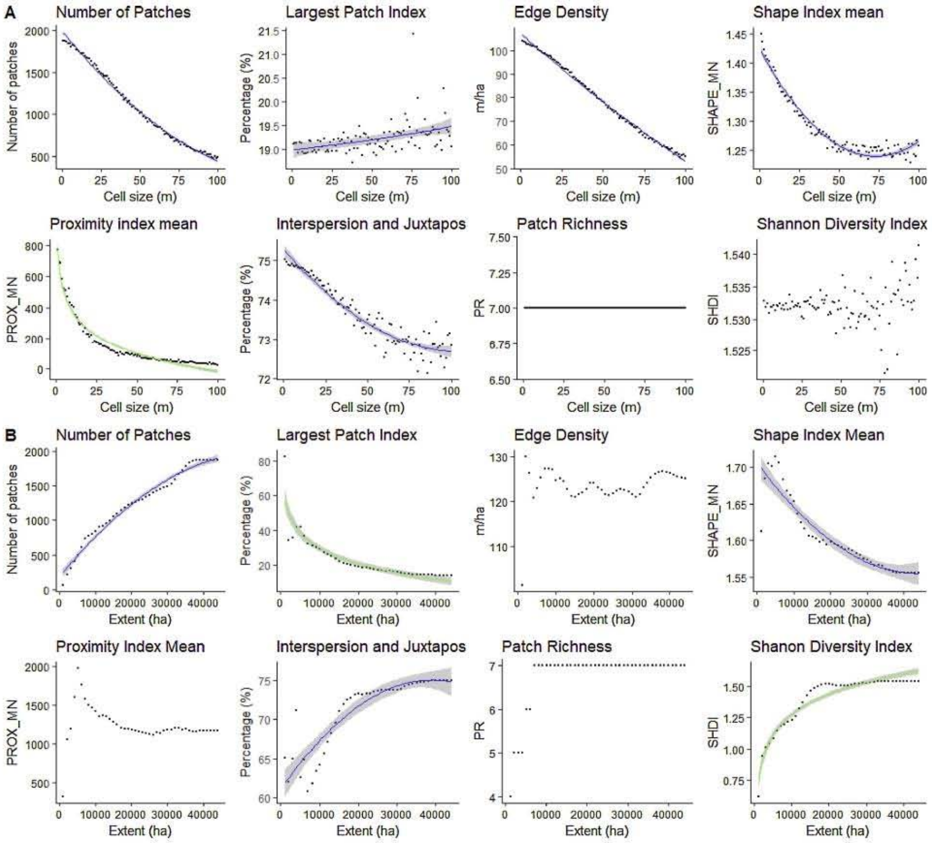

Fig. 2. Scalograms showing the effects of changing grain size (a) and extent (b) on landscape metrics for Zaachila. For scalograms with type 1 (consistent scaling relations) we present in green logarithmic fits and in blue power law fits. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Table 2
Categories of behaviors observed in scalograms for landscape level.

Scale change	Metric	Response	Scaling relationship	Direction
Grain size	NP	Type 1	Power law	Decreasing
Grain size	LPI	Type 1	Power law	Increasing
Grain size	ED	Type 1	Power law	Decreasing
Grain size	SHAPE_MN	Type 1	Power law	Decreasing
Grain size	PROX_MN	Type 1	Logarithmic	Decreasing
Grain size	IJI	Type 1	Power law	Decreasing
Grain size	PR	Type 3	–	–
Grain size	SHDI	Type 4	–	–
Extent	NP	Type 1	Power law	Increasing
Extent	LPI	Type 1	Logarithmic	Decreasing
Extent	ED	Type 4	–	–
Extent	SHAPE_MN	Type 1	Power law	Decreasing
Extent	PROX_MN	Type 4	–	–
Extent	IJI	Type 1	Power law	Increasing
Extent	PR	Type 2	–	–
Extent	SHDI	Type 1	Logarithmic	Increasing

techniques for low-input polyculture, pest-management and soil and water conservation (Altieri et al., 2015; González González, 2018; Rogé et al., 2014; Rogé and Astier, 2015). These practices and techniques have also been shown to be key for the reproduction of biocultural diversity and for the exercise of basic human rights (CEMDA, 2017; Gavin et al., 2015; Lyver et al., 2019).

It is noteworthy that half of the metrics had scalograms exhibiting similar behavior at the landscape level for Zaachila and for other agricultural landscapes previously studied (Teng et al., 2016; Wu, 2004; Wu et al., 2002; Zhang and Li, 2013; Zhang et al., 2007) (Supplementary Material Table 7). This is the case for number of patches, largest patch index and edge density for grain size change. Number of patches, edge density and patch richness also showed the same behaviors for the change in extent. These results point to a set of metrics that are likely to be robust and reliable for their use in a wide range of landscapes differing in geography, land use management and history of management (Supplementary Material Table 7). In contrast, the other half of the landscape metrics exhibited qualitatively different behaviors between this study and others in response to scale change, such as shape index mean and Shannon's diversity index. Most of the differences were between erratic or staircase-like responses in other studies but that

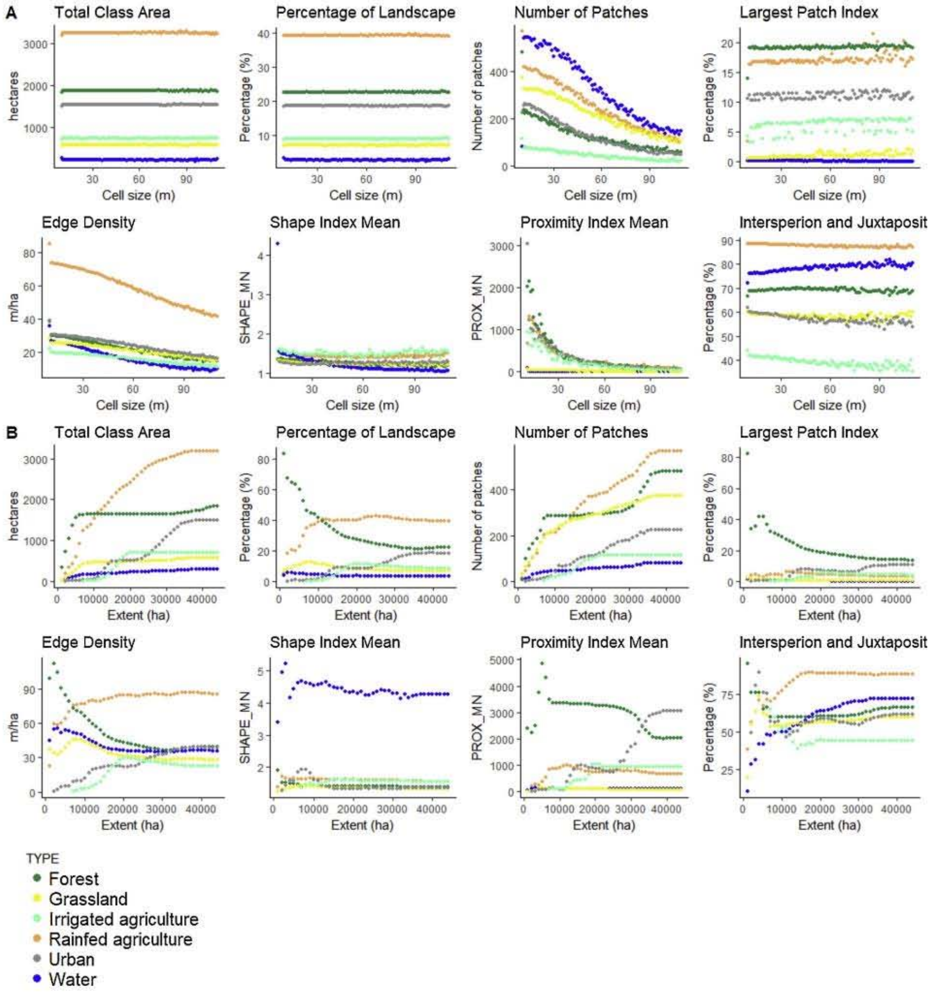

Fig. 3. Scalograms showing the effects of changing grain size (a) and extent (b) on the class metrics taken for Zaachila's land use and vegetation map. Since the behavior types for class level are highly different from class to class the classification was different and it is not possible to graphic the strongest scaling relations.

presented consistent scaling relations in Zaachila. The different behavior of this group of metrics highlights the importance of further testing metric behavior in contrasting landscapes shaped by divergent geophysical and social contexts.

Taking into consideration the metrics and their behaviors at different scales, the most appropriate metrics for a study will depend strongly on the goals of each study. For comparative research between landscapes with different geography and management history, in which metrics may not have been calculated at the same scale, we propose to focus on metrics that are sensible enough to show differences across landscapes, but that are invariant to scale change (type 3). Metrics with consistent scaling relations (type 1) could be somewhat useful given that metric changes based on scale can be anticipated and that their sensitivity to scale change (CV and residuals) is small or moderate (Supplementary Material Table 4, Figs. 1 and 2). In order for these metrics to be useful, their behaviors must be robust, that is, they must show similar behavior in landscapes with very different geography, geomorphology, land use management and history of management. If the metrics comply with these characteristics, we can assume a simple relation between the metrics, no matter the scale at which they were taken. In this study, metrics that had these characteristics include the number of patches, interspersion and juxtaposition index and largest patch index. The last two have small CV values, which also indicates that they are metrics with relatively low sensitivity to scale change (Supplementary Material Table 4). These three metrics were useful for describing landscape fragmentation and class dominance and differed between Zaachila and other landscapes (Fig. 4). They had behaviors type 1 and 3 (Figs. 2 and 3), i.e., behaviors that make these metrics robust across different agricultural landscapes (Teng et al., 2016; Wu, 2004; Wu et al., 2002) and had low sensitivity to scale change

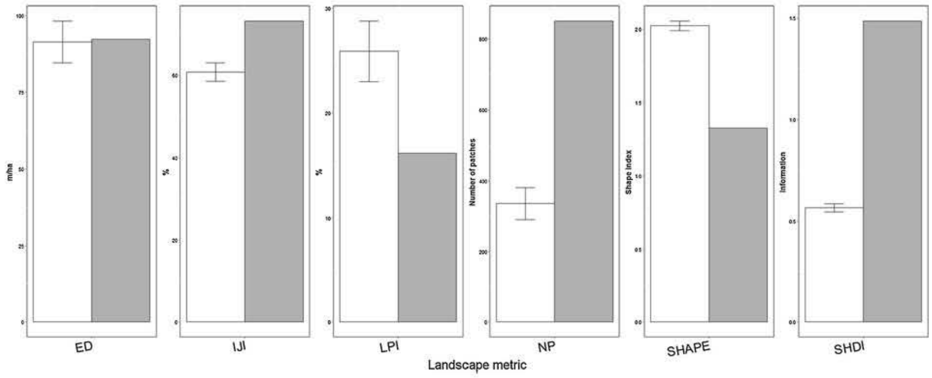

Fig. 4. Bar graph comparing six landscape metrics from Zaachila versus thirteen different landscapes from the United States of America. The y axe is a compound of all the possible values of the different landscape metrics.

(Supplementary Material Tables 4 and 7).

For studies aiming to describe the quality of the matrix, we propose metrics that reveal more information about connectivity, fragmentation per se, diversity and permeability of the classes, such as percentage of landscape, edge density, and interspersion and juxtaposition index, as they jointly reflect how a given matrix facilitates or hinders migration and re-colonization of habitat patches or remnants. Information beyond the landscape metrics is necessary for the assessment of the matrix quality, particularly information on the concrete activities that are performed on each class and how they affect the ecological processes of the species in question. Nevertheless, landscape metrics helped us identify the class with the biggest potential, as given by its spatial distribution, to improve the quality of the matrix if activities aimed at improving its permeability are performed within it (Watling et al., 2011).

In terms of which scale should be used in future works that address how landscape features affect agricultural plots (e.g. Avelino et al., 2012; Connelly et al., 2015; Poveda et al., 2012), we found no optimal scale for the landscape level metrics. For the class level metrics, a grain size below 60 m is recommended, while the change of extent shows a pattern in which the metrics stabilize for all classes from 300 km^2 onwards. Stabilization is desirable for comparisons among different landscapes because it allows comparing them knowing that the metrics will be robust. However, for studies within a single landscape it is interesting to retain variation among classes, so the best scale for studies within Zaachila's municipality and similar landscapes should be smaller than 300 km2. This also suggests that a change in hierarchical structure happens at 300 km^2 in this landscape (Wu, 2013; Zhang and Li, 2013). However, the results obtained for changes in extent scale must be taken with care because they are highly dependent on the starting point of the smallest extent.

It is important to consider some of the limitations of this study. First, the shape of Zaachila's polygon is one of them, given that it has an irregular shape. Some of the agricultural landscapes studied before are also defined by irregular polygons (Teng et al., 2016; Zhang and Li, 2013) but most are squared landscapes (Cardille et al., 2017; Wu, 2004; Wu et al., 2002). This is particularly relevant for extent scalograms, since the elongated shape could be affecting the metrics value as the landscape is covered by continuously larger boxes. Second, it is also necessary to highlight that more than 150 other metrics have been developed to describe landscapes and that they would also need to be examined in terms of their stability with scale changes. Although it is true that many landscape metrics are highly correlated (Wu et al., 2002), it is still necessary to characterize the correlation among this large set of potential metrics in the type of landscape that we studied here. Finally, we think this kind of studies should also take into account the effects of different time scales on the metric behavior. For example, in Zaachila the main land use is rainfed agriculture, which is largely modified by peasants and other actors throughout seasons, years and decades, so that the values of the landscape metrics could exhibit non-trivial dynamics along time points.

Altogether, the measured diversity, complexity and potential connectivity of the Zaachila landscape reveals how different the composition and configuration of a subtropical and peasant-managed landscape can be in comparison with the more industrial agricultural landscapes of temperate regions that have been the main focus of studies on agricultural landscape heterogeneity. It has been shown that these differences in compositional and configurational heterogeneity can impact agricultural management practices (e.g. biological control strategies: Avelino et al., 2012; Connelly et al., 2015; Poveda et al., 2012; Thies and Tscharntke, 1999), persistence and conservation of native biodiversity (Burel, 1989; Chust et al., 2003; Connelly et al., 2015; Fahrig, 2003; Franklin and Lindenmayer, 2009; Gallé et al., 2019; Katayama et al., 2014; Ramos et al., 2018; Reis Madeiros et al., 2019; Rundlöf and Smith, 2006; Smith et al., 2010), agrobiodiversity reproduction (Avelino et al., 2012; Connelly et al., 2015; Weibull, 2003) and ecosystem services such as water availability, soil quality, quality-food provisioning and overall human well-being (e.g. Gallé et al., 2019; Ickowitz et al., 2014; Laudon et al., 2016; Mora Van Cauwelaert, 2016).

Indeed, our results suggest that Zaachila's landscape involving a highly heterogeneous agricultural matrix conformed mainly by rainfed agriculture has a great potential for biodiversity conservation if agricultural practices that increase the permeability of the matrix are maintained or promoted (e.g. pesticide-independent practices; Altieri et al., 2015; CEMDA, 2017; Gavín et al., 2015; González González, 2018; Lyver et al., 2019; Rogé et al., 2014; Rogé and Astier, 2015). Such high permeability would facilitate migration among habitat patches, and ultimately, the maintenance of metapopulations. Moreover, practices associated to high permeability in our study area also contribute to the reproduction of the local biocultural diversity (González González, 2018; Lyver et al., 2019; Mora Van Cauwelaert, 2016). We can also conclude that formally studying spatial heterogeneity through landscape metrics is essential to characterize agricultural matrices, compare them and link landscape structure to potential strategies for sustainable agriculture and biodiversity conservation.

Declaration of Competing Interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2019.106797.

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