



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD

**BALANCES ENTRE LA CONSERVACIÓN Y LA PRODUCCIÓN AGROPECUARIA
EN PAISAJES TROPICALES MODIFICADOS POR ACTIVIDADES HUMANAS**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS BIOLÓGICAS

PRESENTA:

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MORELIA, MICHOACÁN, JUNIO, 2021



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Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 19 de abril de 2021 se aprobó el siguiente jurado para el examen de grado de DOCTOR EN CIENCIAS del estudiante WIES GERMÁN con número de cuenta 517491373 con la tesis titulada "BALANCES ENTRE LA CONSERVACIÓN Y LA PRODUCCIÓN AGROPECUARIA EN PAISAJES TROPICALES MODIFICADOS POR ACTIVIDADES HUMANAS", realizada bajo la dirección del DR. MIGUEL MARTÍNEZ RAMOS, quedando integrado de la siguiente manera:

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

ATENTAMENTE

"POR MI RAZA HABLARÁ EL ESPÍRITU"

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Resumen general:

Los paisajes modificados por actividades humanas (PMH) emergen como posibles áreas para conservar biodiversidad y mantener funciones y servicios ecosistémicos. En gran parte de estos paisajes se desarrollan sistemas de producción agropecuarios (SPA), los cuales experimentan actualmente una homogenización de cultivos con alta carga de insumos. La necesidad de conservar en los PMH se opone a la compleja realidad existente en estas áreas, las cuales, al momento, demandan más tierras para la producción. Para conciliar estas opuestas posiciones es necesario analizar los componentes de conservación (en áreas de bosque remanentes) y producción (en los SPA) e integrarlos con el objetivo de explorar estructuras del paisaje que permitan balances positivos entre la conservación y la producción. En el capítulo 2 se estudia el componente de conservación analizando los cambios en variables ecológicas (biodiversidad, funciones y servicios ecosistémicos) a través de un gradiente de PMH que comprenden entre ~0% y 100% del proceso de conversión de selvas a SPA. El componente de producción se estudia en el capítulo 3, donde se analizan cómo interactúan factores biofísicos, agronómicos y socioeconómicos, a través de las decisiones de manejo de las personas que modulan los PMH, determinando el tipo de sistema de producción de maíz y sus rendimientos. En el capítulo 4 se aborda el componente de integración a través de modelos de optimización multi-objetivos (o modelos de optimización Pareto óptimo), se identifican configuraciones de SPA que maximicen las áreas de bosque y además maximicen los ingresos económicos derivados de la producción a través de estrategias alternativas de intensificación sustentable. Finalmente, en el capítulo 5 se presenta una discusión general de los resultados relevantes encontrados y las conclusiones que se derivan de los mismos.

En los PMH, mantener niveles de diversidad de especies arbóreas comparables a paisajes totalmente cubiertos requieren al menos de 40% de cobertura de bosques independientemente su configuración espacial. Sin embargo, para mantener funciones y servicios ecosistémicos como la producción de biomasa y el almacén de Carbono, es necesario mantener coberturas de selva muy superiores ya que estos atributos disminuyen exponencialmente con la deforestación. En relación a la producción, los sistemas de cultivo de maíz, responden a factores biofísicos como la calidad de suelo. Los campesinos toman decisiones de manejo agronómico en respuesta a las diferencias biofísicas del lote (e.g. incrementando las dosis de fertilizantes). Sin embargo, las herramientas aplicadas no se traducen en mayores rendimientos. En consecuencia, existe inconsistencia entre las decisiones de manejo de los cultivos y el efecto sobre los rendimientos. Por último, el análisis de integración a través de la optimización de Pareto óptimo, mostró que existen configuraciones de SPA que permiten aumentar las áreas de selva y aumentar los ingresos económicos en los PMH. Sin embargo, las configuraciones iniciales, propias de los SPA, deriva en vías de optimización particulares para cada caso. En aquellos SPA con alta intensificación derivada de insumos químicos, aumentar áreas de bosque e ingresos, solo es posible a través de incrementar insumos externos. Sin embargo, en SPA que inicialmente fueron menos intensificados, es posible incrementar áreas de bosque e ingresos a través de prácticas de intensificación sustentable. Los resultados de este estudio doctoral indicarían que aquellos SPA con mayores extensiones y mayores rendimientos basados en utilización de insumos agrícolas no necesariamente fueron los que mayor proporción de selva mantuvieron. En contraposición a la idea de intensificar con insumos, para conservar, se

postula la idea de “integrar para producir conservando” y así conciliar la conservación y la producción en lo PMH.

General summary:

Human Modified Landscapes (HML) emerge as possible areas to conserve forest biodiversity and maintain ecosystem functions and services. Agricultural production systems (APS) are immersed in a large part of these matrices. APS are currently experiencing a homogenization of crops with a high of input of agrochemicals. The need to conserve in the HML is opposed to the complex reality existing in these areas, which demand more land for production. To reconcile these opposing positions, it is necessary to analyse the components of conservation (in remaining forest areas) and production (in APS) and integrate them with the objective of exploring structures of HML that allow positive balances between conservation and production. In chapter 2 the conservation component is studied by analysing the changes in ecological variables (biodiversity, ecosystem functions and services) through a gradient of HML that comprise between ~ 0% and 100% of the forest-to-agriculture process. The production component is studied in chapter 3, where biophysical, agronomic and socioeconomic factors interact, through the management decisions of stakeholders who modulate the PMH, determining the type of maize cropping system and maize grain yields. In chapter 4 the integration component is addressed through multi-objective optimization models (or Pareto optimal optimization models). APS configurations are identified that maximize forest areas and also maximize the economic income derived from agricultural production through alternative sustainable

intensification strategies. Finally, Chapter 5 presents a general discussion of the relevant results found and the conclusions derived from them.

In HML, maintaining levels of tree species diversity comparable to fully covered landscapes requires at least 40% forest cover regardless the spatial configuration. However, to maintain ecosystem functions and services such as biomass production and carbon storage, it is necessary to maintain much higher forest covers since these attributes decrease exponentially with deforestation. In relation to production, maize cropping systems respond to biophysical factors such as soil quality. Farmers apply agronomic management decisions in response to biophysical differences in the field (e.g. increasing fertilizer doses). However, the tools applied do not translate into higher yields. Consequently, there is inconsistency between cropping management decisions and the effect on grain yields. Finally, the integration analysis through the Pareto optimal optimization showed that there are APS configurations that allow increasing the forest areas and increasing the economic income in the HML. However, the initial configurations, typical of the APS, derive in particular optimization pathways for each case. In those APS with high intensification derived from chemical inputs, increasing forest areas and incomes is only possible through increasing external inputs. However, in APS initially less intensified, it is possible to increase forest areas and incomes through sustainable intensification practices. The results of this doctoral study would indicate that those APS with greater extensions and higher yields based on high agrochemical inputs were not necessarily the ones that maintained the highest proportion of forest. In contrast to the idea of intensifying with agrochemical inputs, to conserve, the idea of “integrating to produce while conserving” is postulated and thus reconcile conservation and production in the HML.

Capítulo 1: Introducción general

1.1. Introducción general

Desde principios del siglo XX ha aumentado el conflicto socio-ecológico de escala global entre la producción de alimentos, fibras y, más recientemente, de bioenergía y la conservación de los ecosistemas naturales (Foley et al., 2005). Por un lado, la humanidad demanda mayores volúmenes de estos productos para satisfacer el creciente consumo de una población que alcanzará los 9 millones de personas en el 2050, y por otro lado, se presenta una extensa y rápida conversión de ecosistemas naturales hacia áreas agropecuarias, con la consecuente pérdida de biodiversidad y de funciones y servicios que estos ecosistemas proporcionan a las sociedades humanas (Foley et al., 2013; Niklasson et al., 2006). Este conflicto se acentúa en los bosques tropicales húmedos (o selvas húmedas), debido a la enorme biodiversidad presente en estos ecosistemas, al preponderante papel que estos bosques juegan en el funcionamiento de los ciclos globales del agua, carbono y nutrientes minerales, entre otros, y a la multiplicidad de servicios ecosistémicos que proveen (Costanza et al., 1997; Díaz, 2013).

El presente proyecto doctoral es un intento de abordar este conflicto basándose en distintas disciplinas de investigación. Ecología del paisaje y de comunidades, agronomía a escala de lote/parcela y la modelación de sistemas de producción agropecuaria son las disciplinas que dan sustento teórico-conceptual a este trabajo. El proyecto utilizó como sistema de estudio a la región de La Selva Lacandona. Ubicada al sur del estado de Chiapas (de Vos, 1988), ésta es una de las regiones más emblemáticas de México, por sus selvas de gran biodiversidad y por el rápido proceso de conversión a sistemas agropecuarios que

éstas han sufrido en menos de cinco décadas. A continuación, se presenta una sección de antecedentes, en la que se describen de manera sucinta: i) características de las selvas húmedas, en general, y de México, en particular, ii) Procesos de cambio del uso de la tierra en regiones cubiertas por selvas húmedas, iii) efectos ecológicos de conversión de selvas en sistemas agropecuarios, iv) procesos que ocurren en las áreas agrícolas en los paisajes modificados por actividades humanas y finalmente, v) una propuesta de cómo conciliar la producción y la conservación en los sistemas de producción agropecuarios. Estos aspectos establecen el contexto al planteamiento de los problemas y preguntas de investigación. Luego se exponen los marcos teóricos de la tesis que encuadran cada pregunta de investigación y finalmente se establecen los objetivos general y particulares.

1.2 Antecedentes

1.2.1 Los bosques tropicales húmedos (selvas húmedas)

Las selvas húmedas son los biomas más biodiversos del planeta y se agrupan en cinco grandes regiones, a saber: la selva de Nueva Guinea, la selva del sudeste asiático, la selva de Madagascar, la selva de África central y la selva del Neotrópico (Corlett y Primack, 2011). Todas estas regiones se caracterizan por recibir precipitaciones mínimas de 1,500 milímetros anuales, distribuidas uniformemente, aunque en algunas localidades se presentan períodos de relativa sequía de menos 60 mm mes^{-1} en algunos meses del año (Peel *et al.* 2007; Corlett y Primack 2011). Globalmente, el promedio de lluvia anual pan-tropical, es decir, la media entre las cinco regiones, es de $2,152 \pm 487 \text{ mm año}^{-1}$. Las temperaturas medias anuales de las zonas bajas de estos biomas es $25^{\circ}\text{C} \pm 1^{\circ}\text{C}$ con una

reducida variación estacional entre meses de $3.2\text{ }^{\circ}\text{C} \pm 1^{\circ}\text{C}$ (DS de variación entre las cinco regiones). Estas temperaturas elevadas se deben a la elevada radiación solar incidente que experimentan las zonas entre los trópicos de cáncer y capricornio, de alrededor de 16.8 Mega Joules por metro cuadrado por día ($\text{MJ} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$, Malhi y Wright 2004).

De las cinco regiones, la más extensa y biodiversa es la región del Neotrópico. Esta región ocupa aproximadamente la mitad del área total cubierta por selvas húmedas del planeta y, en términos biogeográficos, se divide en tres sub-regiones: la región que comprende la cuenca del río Amazonas y la cuenca del río Orinoco, las selvas de la costa sudeste de Brasil, denominada Mata Atlántica y, por último, la región que comprende desde el noreste de la costa pacífica de América del Sur (Bolivia, Perú, Ecuador, Colombia y Venezuela) hasta el sur meridional de México (Corlett y Primack, 2011; Hansen et al., 2010; Hansen et al., 2013). Debido a una barrera marina, ésta última permaneció separada del bloque amazónico por 25 millones de años, uniéndose hace tres millones de años con la emergencia del Istmo de Panamá (Corlett y Primack, 2011).

1.2.2. Las selvas húmedas de México

Como se explicó, la región norte de la selva húmeda neo-tropical encuentra a México en sus límites geográficos. Históricamente, estas selvas, comprendían, cerca del 9.2% del territorio terrestre del país (1.931 millones de km^2), abarcando los estados de Veracruz, Tabasco, Oaxaca, Chiapas, Campeche, Yucatán y Quintana Roo. En términos biogeográficos esta superficie se divide en cuatro provincias caracterizadas por climas húmedos a sub-húmedos: Tamaulipeca, Golfo de México, Yucateca y Petén (Dirzo et al., 2009; Soberón et al., 2008). Según el mapa de uso de suelo del INEGI, serie V,

(<http://www.inegi.org.mx/geo/contenidos/reclnat/usuarios/>), para el 2011, México contaba con una superficie de 1,321,408.61 ha de bosques tropicales perennifolios y 57,576.18 ha de bosques tropicales sub-perennifolios (Fig. 1.1), sumando un total de 1,378,984.8 ha en conjunto, equivalente a menos del 1% del territorio terrestre del país.

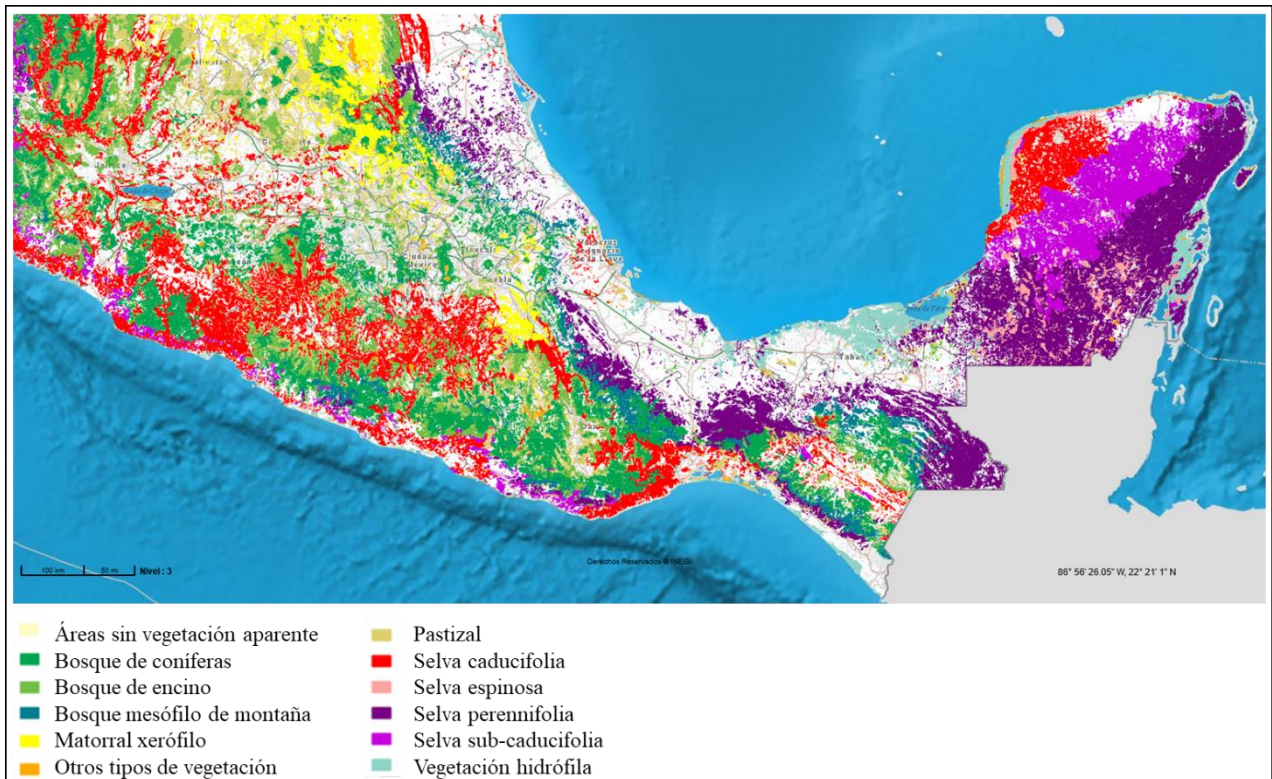


Figura 1.1. Mapa de uso del suelo del centro-sur de México, 2011 (<http://gaia.inegi.org.mx/>). Gran parte de las áreas sin vegetación aparente (ahora cubiertas por diferentes sistemas agropecuarios) estuvieron cubiertas hasta hace menos de un siglo por selvas húmedas.

En sus extremos este y sur la se encuentra la provincia biogeográfica del Petén, que se extiende entre México, Guatemala y Belice, delimitándose por la Sierra de los Cuchumatanes hasta la Bahía de Amatique (Soberón et al., 2008). En el Petén, hacia el este del estado de Chiapas, se encuentra una de las regiones de selva húmeda más extensas y con mayor biodiversidad en México, la región de “La Selva Lancandona” (Carabias et al.,

2015; Carabias et al., 2000). En términos geo-políticos la región comprende los municipios de Palenque, Chilón, Altamirano, Ocosingo, Las Margaritas y La Independencia (Farías Campero y Vásquez Sánchez, 1996). El área cubierta de selva comprendía una extensión, en el año 2000, de alrededor 1,320,000 ha y hacia 2012 se redujeron a 1,094,000 ha (Carabias et al., 2015). En el presente la región con mayor cobertura de selva, se enmarca en la reserva de la biosfera “Montes azules” (Fig. 1.2).

1.2.3. La selva Lacandona y la región de Marqués de Comillas

La selva Lacandona debe su nombre a la comunidad indígena que allí vivía desde los tiempos pre-hispánicos, es decir los lacandones (de Vos y Marion, 2015). Actualmente se reconocen cinco subregiones de la Selva Lacandona: la subregión Norte, las Cañadas de Margaritas, las Cañadas de Ocosingo, la Comunidad Lacandona, y Marqués de Comillas. Delimitada por los ríos Lacantúm, al oeste, y Usumacinta al norte y este, y por el límite con Guatemala, al sur, Marqués de Comillas ocupa la parte oriental de la Selva Lacandona. Esta región se conforma de dos municipios, Marqués de Comillas y Benemérito de las Américas y abarca una superficie de 2,032 km² (Fig. 1.2; Castillo-Santiago, 2009). Las precipitaciones anuales en esta región alcanzan los 3000 mm y las temperaturas mensuales promedian los 22°C (Martínez-Ramos et al., 2009). El relieve es relativamente plano, con presencia de lomas suaves y la composición y estructura de la vegetación es típica de selvas húmedas (Carabias et al. 2015; Navarrete-Segueda et al. 2018).

La región de Marqués de comillas tiene una larga historia de presencia humana. La civilización maya ocupó esas tierras hace más de 1.300 años. Luego de la conquista, el

grupo lacandón habitó en la región desde hace alrededor 500 años (de Vos y Marion, 2015). Más recientemente entre ~ 1820 y 1950, hubo una fuerte extracción selectiva de árboles de alto valor maderable para su exportación a Europa (de Vos, 1988). Sin embargo, hasta la década de 1970 la región mantenía prácticamente completa la cobertura de selvas húmedas (de Vos y Marion, 2015). Un programa de colonización iniciado a finales de la década de 1970 promovió el establecimiento de nuevas comunidades. Así, Marqués de Comillas experimentó un proceso de migración de personas de diferentes estados de México (Chiapas, Guerrero, Jalisco, Michoacán, Oaxaca, Tabasco) y Guatemala.

Paralelamente, incentivos federales, promovieron, principalmente la ganadería extensiva, lo que condujo a una rápida deforestación (Carabias et al. 2015). Actualmente, ~ 70% de la región está cubierta por múltiples y diversos usos de suelo como pastos para ganado, campos de cultivo, plantaciones comerciales, parches de bosque secundario y asentamientos humanos (Zermeño-Hernández et al., 2016). Para el año 2018, el portal de monitoreo de usos de suelo Mad-Mex (<https://madmex.conabio.gob.mx/>) reportó que la región de Marqués de Comillas mantenía solo el 33.53% de cobertura de selva. Así esta región se presenta como un escenario adecuado para analizar las preguntas de investigación que tienen que ver con los Paisaje modificados por actividades humanas (Melo et al., 2013).

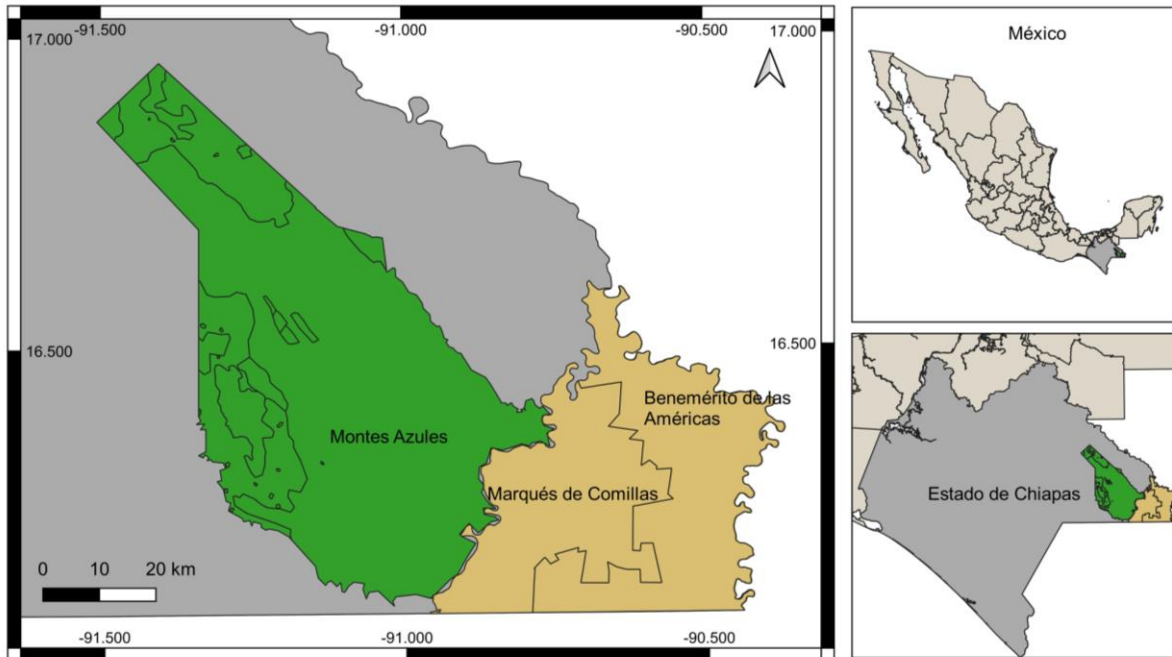


Figure 1.2: Subregiones de la “Selva Lacandona”. Reserva de Montes Azules (Verde) y región de Marqués de Comillas (marrón) conformada por los municipios de Marqués de Comillas y Benemérito de las Américas. La región de Marqués de Comillas se utilizó como sitio de estudio de los “Paisajes modificados por actividades humanas”.

1.2.4. Procesos de cambio del uso de la tierra en regiones cubiertas por selvas húmedas

A principios de siglo, las predicciones acerca de los factores con mayor impacto sobre la biodiversidad en los ecosistemas terrestres mencionaban: el aumento de CO₂ atmosférico, el cambio climático global, la pérdida de vegetación nativa, el aumento en los niveles de deposición de nitrógeno y el cambio de uso del suelo (Sala et al., 2009). A pesar de la enorme incertidumbre que existía acerca de las interacciones entre estos factores sobre la biodiversidad, ya se identificaba al cambio de uso del suelo como el factor que más impacta

a cualquier ecosistema terrestre y, en especial, a los bosques tropicales (Foley et al., 2005; Sala et al., 2009).

El cambio climático global parece haber acaparado la atención en el estudio de la biodiversidad ya que los artículos científicos que se refieren a este fenómeno como una amenaza a la biodiversidad aumentaron exponencialmente (Titeux et al., 2017). Sin embargo, el Panel Intergubernamental sobre Biodiversidad y Servicios Ecosistémicos (IPBES), en su último reporte de evaluación global de la diversidad menciona que desde la década de 1970 la producción agrícola ha aumentado pero la mayoría de las contribuciones de la naturaleza a la especie humana han disminuido. Esta disminución de las contribuciones de la naturaleza se deben, como primer factor, al cambio en el uso de la tierra seguida de la sobre-explotación directa de organismos vivos (Díaz et al., 2019). En coincidencia, estos dos factores aparecen como los primeros en amenazar las especies en riesgo de extinción a escala global (Maxwell et al., 2016).

Las actividades más importantes del cambio del uso del suelo a escala global es la conversión de bosques, selvas, sabanas, pastizales y estepas en cultivos anuales y perenes, en pastizales mono-específicos para ganadería y para el establecimiento de áreas urbanas (Asner et al., 2004; Foley et al., 2005; Ricciardi et al., 2018b). Este proceso de conversión ha sido descrito en el continente Americano (Guevara y Laborde 2008), tanto en las selvas de la Amazonía; en Brasil, Bolivia, Perú y Ecuador (Banks-leite et al., 2014; Flamenco-Sandoval et al., 2007; Foley et al., 2007; Lerner et al., 2014; Mccracken et al., 1999), como en las selvas de Mesoamérica, sobre todo en México y Belice (Arroyo-Rodríguez et al., 2015; Challenger y Dirzo, 2009; Lambert y Arnason, 1986).

El proceso de conversión de ecosistemas naturales a sistemas agropecuarios no es lineal y puede estar asociado con cambios en los recursos biofísicos y en el sistema social. Estas transiciones pueden originarse por retroalimentaciones socio-ecológicas negativas, por ejemplo, por agotamiento de recursos clave o de cambios socioeconómicos independientes al sistema ecológico, por ejemplo, la globalización de la economía y la producción de consumibles (Lambin y Meyfroidt, 2010). En el trópico, un conjunto complejo de factores sociales, políticos y económicos han promovido la conversión de selvas maduras a sistemas de producción agrícola simplificados, basados generalmente en cultivos mono-específicos anuales (maíz, soya o pasturas anuales para el ganado) o perennes como el eucalipto, la palma africana de aceite (*Elaeis guineensis*) y la caña de azúcar (Meyfroidt et al., 2014; Ricciardi et al., 2018a; Sodhi et al., 2010).

En México, el impacto de las reformas neoliberales a partir del acuerdo NAFTA (tratado de libre comercio, entre México, Estados Unidos y Canadá) en 1994, que promovieron la expansión e intensificación de los sistemas de producción ganadera y maíz extensivos, aumentaron la pérdida de selvas y bosques. Más recientemente la expansión de forestaciones como la palma africana de aceite y el aguacate (*Persea americana*, Castellanos-Navarrete and Jansen 2015; Cho *et al.* 2021) acentuaron este proceso a pesar del aumento de la cobertura arbórea enmascarado por la expansión de estos cultivos (Bonilla-Moheno y Aide, 2020).

1.2.5. Efectos ecológicos de conversión de selvas en sistemas agropecuarios en paisajes modificados por actividades humanas

Se pueden identificar tres principales consecuencias ecológicas de la conversión de bosques a la agricultura simplificada. La primera es la pérdida de la **biodiversidad (B)**, en particular de las “especies especialistas de bosque maduro” y especies endémicas (Banks-Leite *et al.* 2014; Martínez-Ramos *et al.* 2016; Zermeño-Hernández *et al.* 2016). En el paisaje modificado, algunas especies animales y vegetales generalistas (adaptados a disturbios) pueden persistir pero otras especies, cuyo hábitat se encuentra en el bosque maduro y son muy vulnerables a las perturbaciones severas, son propensos a la extinción local (Banks-leite *et al.*, 2014; de Castro Solar *et al.*, 2015). Sumado a la pérdida de la biodiversidad, la diversidad cultural se ve amenazada cuando los sistemas de cultivo tradicionales desarrollados por la población local (en estrecha relación con los bosques naturales) son reemplazados por técnicas agrícolas modernas o convencionales. La nueva cultura adquirida también implica nuevas formas de cuidado de la salud y educación, que generalmente conduce a la erosión del lenguaje, disminución de la transferencia de conocimientos culturales y un cambio en las bases de conocimientos locales (Angelsen y Kaimowitz, 2001; Carson *et al.*, 2018; Pilgrim *et al.*, 2009; Rodrigues *et al.*, 2009).

La segunda consecuencia de la conversión de los bosques a la agricultura es la modificación de las **funciones del ecosistema (EF)**, por sus siglas en inglés), en particular de aquellas relacionadas con la producción primaria. La pérdida de hábitat implica la pérdida en diversidad de especies. A mayor diversidad de especies mayor es la diversidad de diferentes rasgos funcionales relacionados con la productividad primaria, la producción y la descomposición de hojarasca (Lohbeck *et al.*, 2016). Recientemente se ha demostrado

que existe una relación convexa y positiva entre la biodiversidad y la productividad para los bosques en general (Liang et al., 2016a) y para las selvas tropicales en particular (Poorter et al., 2015). Estas relaciones permiten comprender la íntima conexión que existe entre la diversidad de especies y el equilibrio dinámico de sus abundancias poblacionales sobre las funciones del ecosistema y en consecuencia los servicios ecosistémicos. Las selvas húmedas tropicales almacenan alrededor del 25% del carbono total del planeta y aportan más de un tercio de la productividad primaria neta total de los ecosistemas terrestres (Bonan, 2008; Dixon et al., 1994). Estimaciones sobre el efecto relativo del aumento de la concentración de CO₂ atmosférico, de la temperatura, del cambio en los regímenes de lluvia y la deforestación muestran que ésta última es, y será en el futuro, la mayor causa de pérdida de la capacidad de capturar carbono de los bosques tropicales (Cramer et al., 2004; Mitchard, 2018).

Por último, la tercera consecuencia de la conversión de selvas a la agricultura es el cambio en variedad, cantidad y calidad de los **servicios de los ecosistemas o servicios ecosistémicos (ES**, por sus siglas en inglés ; Harvey *et al.* 2008; Arroyo-Rodríguez *et al.* 2015; Balvanera *et al.* 2016). La pérdida de especies de árboles puede alterar los procesos clave de los ecosistemas y los importantes servicios que proveen, ya que al igual que las funciones del ecosistema, diferentes especies de plantas contribuyen a un amplio espectro de servicios de regulación, provisión y soporte (Balvanera et al., 2016). Se ha demostrado que los servicios de soporte y regulación de los ecosistemas, como la formación del suelo, la regulación del ciclo de los nutrientes y del agua, la productividad primaria, el almacenamiento de C, la regulación de la calidad del aire, la regulación de la erosión, y la

protección contra huracanes, se encuentran en mayor oferta en bosques primarios que en bosques secundarios o en campos agrícolas (Alamgir et al., 2016; Ferraz et al., 2014).

Como un ejemplo de lo anterior, en las selvas de Colombia el 9% de carga de sedimentos en la cuenca del río Magdalena fue debido a la deforestación, representando 482 millones de toneladas de sedimentos en las últimas tres décadas (Restrepo, 2015). Por otro lado, el aumento de los cultivos agrícolas, que no son dependientes de animales polinizadores, ha resultado en una reducción en la demanda de polinizadores, afectando a los cultivos que si son estrictamente dependientes de ellos. Se ha reportado una relación estrecha entre la abundancia y diversidad de polinizadores y el rendimiento de los cultivos (dependientes de polinizadores) en Francia e Indonesia (Deguines et al., 2014; Sodhi et al., 2010). La deforestación y la fragmentación cambian el hábitat de varias especies que están interconectadas a través de las cadenas tróficas. Especies “enlace-móvil” (es decir, especies que se mueven activamente en los paisajes a través de hábitats conectados), están amenazadas y pueden llegar a mermarse o extinguirse con el aumento de la deforestación y la fragmentación (Banks-Leite *et al.* 2014). La disminución de estas especies a su vez puede afectar a las redes tróficas, causando efectos en cascada o alterando procesos como la regeneración del bosque y la funcionalidad de todo el ecosistema (Gardner et al., 2009).

1.2.5.1. Planteamiento del problema de estudio 1

La expansión de sistemas de producción agropecuarios simplificados, que abastecen tanto los mercados locales como globales, siguen diversas e intrincadas vías de conversión de cambio de uso de la tierra. El avance en la frontera agrícola implica deforestación directa e indirecta y tiene como resultado varios impactos sociales y ambientales (Meyfroidt et al., 2014). Surge así, un importante desafío de investigación relacionado con poder determinar

hasta qué punto es posible deforestar manteniendo niveles de B, EF y ES que aseguren la permanencia, calidad y vitalidad de las selvas húmedas en los paisajes modificados por actividades humanas (PMH).

Trabajos como el de Gardner *et al.* (2009), Melo *et al.* (2013) y Arroyo-Rodríguez *et al.* (2015) han propuesto marcos conceptuales que permiten explorar, por un lado, factores clave que impactan la dinámica de PMH y, por el otro lado, las relaciones existentes entre la biodiversidad, la producción de alimentos y los balances de energía en estos paisajes. Estos estudios coinciden en que la conservación de porciones de bosques maduros y/o de bosques secundarios es crítica para la calidad de los ecosistemas en los PMH, en términos biológicos, sociales y económicos. Para identificar paisajes que mantengan considerables niveles de B, EF y ES en los PMH, sería necesario analizar qué trayectorias de cambio experimentan variables indicativas de estos componentes de conservación a medida que cambia el porcentaje de cobertura de remanentes de bosques (composición del paisaje) y se modifica la organización espacial de estos fragmentos (configuración del paisaje) al aumentar las áreas agrícolas.

1.2.6. Procesos que ocurren en las áreas agrícolas en los paisajes modificados por actividades humanas

Hasta ahora se han descrito consecuencias ecológicas relacionadas con la conversión de bosques en áreas de producción agrícola simplificadas. Para una aproximación más completa de la dinámica de los PMH es necesario involucrar al análisis las áreas de producción agrícola. El sistema de producción agropecuario tiene como unidad de estudio a

la porción de tierra sobre la cual el productor/a, granjero/a, campesino/a o ejidatario/a (según el país donde se desarrolle) tiene dominio y toma decisiones (Stanton, 1991). En estos sistemas no sólo operan procesos ecológicos, también operan procesos productivos y factores socioeconómicos y culturales que tienen un fuerte efecto sobre la dinámica del paisaje en conjunto.

Los sistemas de producción en México son tan diversos como su geografía y ecosistemas. Una característica común a ellos es el tamaño. El 74% total del área de producción agrícola de México se caracteriza por desarrollarse en unidades de producción pequeñas a medianas, entre 0 y 50 ha. Este subconjunto produce más de la mitad de energía y alimentos del total de producción del país (Ricciardi et al., 2018a; Samberg et al., 2016). Dos de las actividades más frecuentes son la ganadería y la agricultura. Dentro de ésta última, el cultivo de maíz (*Zea mays L.*) es el predominante y más representativo por haberse originado a través de la domesticación en estas tierras. Esto favoreció que el maíz, sea la base alimenticia del país y presente una enorme herencia cultural relacionada a los modos de vida y a sus diferentes formas de manejo (Casas et al., 2016).

En la tabla 1 se muestran las especies anuales y perennes cultivadas según la encuesta anual agropecuaria de 2019 realizada por el Instituto Nacional de Geografía e Informática (INEGI, www.inegi.org.mx/datos/). Considerando la superficie sembrada de todas las especies, el maíz ocupa el 54% del total del área y si se consideran solo las especies anuales, el 65% del área total sembrada es ocupada por maíz.

Tabla 1.1: Cultivos principales sembrados en México y su superficie según la encuesta anual agropecuaria 2019 (www.inegi.org.mx/datos/).

Cultivos	Especies	Hectáreas sembradas
Anuales	Amaranto	4226.88
	Arroz	26867.95
	Calabaza	54882.70
	Cebolla	43557.56
	Chile	135488.20
	Frijol	1788816.67
	Jitomate (tomate rojo)	42383.32
	Maíz amarillo	1534965.48
	Maíz blanco	6672098.24
	Sorgo grano	1411676.35
	Soya	187766.04
	Trigo grano	702054.95
Perennes	Aguacate	213422.12
	Alfalfa	397487.93
	Cacao	57096.21
	Caña de azúcar	873978.27
	Fresa	13821.19
	Limón	209436.57
	Mango	181665.21
	Manzana	36874.69
	Naranja	443174.04
	Plátano	92834.23
	Uva	28543.91

Los sistemas de producción de maíz pueden variar desde aquellos altamente tecnificados (utilización de maquinaria pesada, uso de híbridos mejorados, dosificación variables y asistencia con mapeo satelital y drones) hasta tradicionales (uso de variedades nativas, con labor manual y en asociación con otras especies como el frijol, calabaza o chile; Ridaura *et al.* 2021). En todos los casos un objetivo común es obtener producto en granos (rendimiento). Sin embargo, la manera de que ésta actividad es llevada a cabo puede potencialmente generar externalidades ambientales y sociales. Se define aquí el término de

“intensificación agrícola” como el incremento de producción por unidad de superficie (en un mismo ciclo o período de tiempo). La intensificación puede lograrse a través de múltiples maneras. Se puede intensificar incrementando los insumos agrícolas, por ejemplo, incrementando rendimientos a través de incrementar dosis de fertilizantes (Matson et al., 1997). Sin embargo, también, se puede intensificar promoviendo y potenciando las funciones y servicios que el ecosistema provee, por ejemplo, aumentando la diversidad de cultivos, manejando los abonos, manteniendo rotaciones de cultivos, aumentando la resiliencia a través de asegurar la auto-provisión de alimento para el ganado y favoreciendo la heterogeneidad global del sistema (Tittonell, 2014). A esta última aproximación, la llamaré intensificación sustentable (Tscharrntke et al., 2012).

1.2.6.1. Planteamiento del problema de estudio 2

Luego de la denominada “revolución verde” a partir de 1960, los sistemas de producción de cultivos duplicaron sus rendimientos (Pellegrini y Fernández, 2018). Este aumento en la producción palió el hambre y la desnutrición presentes en muchos países. Sin embargo, el aumento de la productividad de los cultivos estuvo asociado a un aumento exorbitante de fertilizantes y pesticidas (Tilman et al., 2002). Algunas prácticas desacertadas de estas actividades provoca, por ejemplo, que los nutrientes agrícolas se acumulen en los hábitats acuáticos y terrestres y las aguas subterráneas (Galloway et al., 2003; Galloway et al., 1995). Más aún, el uso inadecuado de pesticidas (insecticidas, herbicidas, fungicidas) produce que a menudo no lleguen a metabolizarse completamente en los cultivos afectando organismos no objetivos como microorganismos del suelo y micorrizas (Druille et al., 2016; Druille et al., 2013; Primost et al., 2017). En los ecosistemas tropicales, estos

impactos se traducen en la reducida capacidad de regeneración de terrenos que son abandonados luego de sucesivos ciclos agrícolas. Se ha mostrado que la intensidad, la extensión y la duración de las actividades agrícolas disminuyen el potencial de regeneración y resiliencia de los ecosistemas (Jakovac et al., 2015; Zermeño-Hernández et al., 2015, 2016).

Para intentar comprender las dinámicas de las áreas de producción dentro de los PMH resulta de importancia analizar los procesos socio-productivos a una escala que permita identificar qué factores están operando y potencialmente impactando a escalas superiores. Estudiar los sistemas de cultivo de maíz (a escala de lote) dentro de los sistemas de producción agropecuarios, dentro de los PMH permitiría identificar cómo las decisiones de manejo (determinadas por los factores biofísicos, agronómicos y socioeconómicos) pueden estar operando en el sistema en conjunto.

1.2.7. Conciliando la conservación y la producción agropecuaria

En la actualidad las relaciones que existen entre las áreas de conservación y de producción agropecuaria se han enmarcado fuertemente en el debate de “land-sharing” (integración de la tierra) vs. “land-sparing” (separación de la tierra). En éste marco, la posición “land-sharing” tiene como premisas la heterogeneidad del paisaje, la resiliencia y las interacciones ecológicas entre las áreas de conservación y las de producción (Green et al., 2005; Kremen, 2015). De ésta manera los paisajes, entendidos como matrices, logran una alta permeabilidad, i.e. que las especies vegetales y animales presentes en los fragmentos prístinos pueden “moverse” (a través de la dispersión, si son vegetales o la migración si son

animales) a través del espacio (Ceccon, 2013; Metzger & Muller, 1996).

Por el contrario “land sparing” se asocia con un modelo de “islas” de paisajes modificados donde las áreas de conservación están separadas del área de producción agrícola, las cuales tienen como objetivo la maximización de los rendimientos brutos (Fischer et al., 2008). Hasta el momento un considerable cuerpo de trabajos científicos abordan el tema de manera conceptual, determinando modelos teóricos matemáticos que podrían ayudar al análisis de algunos casos (Green et al., 2005) o marcos teórico-conceptuales para el entendimiento del caso (Fischer et al., 2008; Kremen, 2015; Perfecto y Vandermeer, 2012).

Existen evidencias empíricas a favor del land-sparing que muestran que la riqueza de especies (de pájaros y plantas anuales) tiende a ser mayor en sistemas donde las porciones de área naturales están separadas de las de producción (Balmford et al., 2005; Egan y Mortensen, 2012; Green et al., 2005; Phalan et al., 2011). Sin embargo, un punto a tener en cuenta a favor o en contra de estas dos posturas sobre el uso de la tierra es la escala considerada para afirmar o no una postura. Por ejemplo, Franklin y David (2016) concluyen posturas a favor de land-sparing pero sus áreas de estudio fueron reducidas (1.6 ha), las cuales se aproximan a un contexto espacial de land-sharing y no de land-sparing. En éste sentido, la escala a la cual se conserva o se produce y la configuración de los distintos usos cobran importancia a efectos de diseñar sistemas de producción agropecuarios y, por ende, paisajes con un relativo equilibrio ecológico sin comprometer biodiversidad, funciones y servicios ecosistémicos que regulan procesos biológicos locales y globales (energía, carbono y agua, Lewis *et al.* 2009).

Por otro lado, los sistemas de producción agropecuarios en el trópico (TFS, por sus siglas en inglés) se han desarrollado en las regiones con mayor biodiversidad terrestre del mundo (Laurance et al., 2014; Malhi et al., 2014). En estas regiones actualmente existe una rápida propagación de cultivos simplificados a gran escala (arroz, soja, aceite de palma y pastos para el ganado) que amenazan no solo a la selva tropical (Ordway et al., 2017; Phalan et al., 2013), sino también a los usos multi-funcionales desarrollados en íntima armonía con la naturaleza, propios de los sistemas tradicionales campesinos e indígenas (Kass y Somarriba, 1999; Toledo et al., 2003). Esta expansión de los monocultivos ejerce presión para reducir los parches de selvas tropicales remanentes y además las prácticas agrícolas tradicionales (Alamgir et al., 2016; Toledo et al., 2003).

Considerando el marco del debate “land sharing” vs. “land sparing”, la literatura muestra que en el trópico, lo que podría estar ocurriendo es una transición del modelo “land sharing” i.e, agricultura campesina con bajos insumos, uso de variedades, razas y cultivares nativos y bajo impacto en el ambiente hacia un modelo productivo “land sparing” i.e. un modelo de islas (cada vez más expandidas) con alta producción bruta, alto uso de insumos (maquinaria pesada, fertilizante y pesticidas) y grandes impactos en el ambiente.

1.2.7.1. Planteamiento del problema de estudio 3

Los sistemas de producción agrícola son necesarios para los seres humanos, puesto que de éstos se extraen productos para el autoabastecimiento y/o para proporcionar de alimentos, fibras y energía a la sociedad urbana, a través del mercado. Los sistemas de producción agropecuarios de pequeña a mediana escala, que potencialmente se enmarcarían en un

modelo “land sharing”, son extremadamente importantes para la seguridad alimentaria, como también lo son para la conservación y diversificación de especies, manejos y costumbres a lo largo de todo el mundo (Ridaura et al., 2021; Sibhatu y Qaim, 2018). Estos sistemas sostienen a más de 380 millones de hogares agrícolas en todo el mundo, producen más del 70% de las calorías alimentarias producidas en las regiones donde están presentes y son responsables de más del 50% de las calorías alimentarias producidas a nivel mundial (Samberg et al., 2016). Particularmente para México los sistemas de producción de pequeña escala han demostrado garantizar seguridad alimentaria a las comunidades rurales en más del 50% de las 7 eco-regiones del país (Galeana-Pizaña et al., 2021).

Hasta el momento, las áreas agrícolas han ganado extensión en detrimento de las áreas de bosque y, en la región del Neotrópico, esta tendencia no parece revertirse (Potapov et al., 2017). La ganadería bovina extensiva en las selvas en centroamérica, la palma aceitera (*Elaeis guineensis*) en Indonesia y la soya (*Glycine max*) en las selvas Atlánticas de Brasil son los ejemplos más representativos de este proceso (Austin et al., 2019; Galvan-Miyoshi et al., 2015; Richards et al., 2012) . Así, estos agricultores pueden estar expuestos a cambiar el uso de la tierra debido a la influencia de los cultivos comerciales y a la presión de los actores a gran escala, la inseguridad en la tenencia de la tierra (Meyfroidt et al.2014), o enfrentar vulnerabilidades a los cambios climáticos con menos recursos para lograr innovación y acciones para adaptación (Bouroncle et al.2017; Donatti et al.2019). Entonces, los TFS se enfrentan con uno de los desafíos más importantes de la producción de alimentos. Este es, producir alimentos para las familias y para la sociedad sin amenazar los parches de selva tropical y sobreponerse a la creciente expansión de monocultivos simplificados.

En los sistemas complejos que involucran objetivos y procesos productivos y ambientales, la interacción de estos componentes pueden comportarse como trade-offs (disyuntivas, funciones que se contraponen) o bien como sinergias. Existen varios modelos de simulación para explorar este tipo de marco a nivel sistema de producción, paisaje y región (Chopin et al., 2015; Groot et al., 2012; Todman et al., 2019). Estos modelos se basan en algoritmos genéticos de optimización multi-objetivo que generan un gran conjunto de alternativas Pareto-optimizadas. Para el caso de sistemas de producción agropecuarios, estos algoritmos generan configuraciones de usos y estrategias alternativas que potencialmente satisfacen las condiciones definidas inicialmente. Al comparar dos objetivos que muestran un trade-off, las situaciones óptimas de Pareto darán como resultado un conjunto de soluciones en la frontera que permiten identificar opciones mejoradas a la situación inicial.

1.3. Preguntas de investigación y marcos conceptual de investigación

Considerando el contexto hasta aquí presentado, la presente investigación doctoral se dirige a explorar cómo un gradiente de deforestación en los PMH afecta componentes ecológicos de las selvas tropicales (capítulo 2). Luego, se explorará cómo las estrategias de manejo de los tomadores de decisiones que habitan en los PMH impactan en la producción, pero también en las potenciales externalidades ambientales en las áreas de producción (capítulo 3). Para este caso se utilizará a los sistemas de cultivo de maíz a escala de lote o parcela como unidad que permite bien describir estas interacciones. Y por último se explorarán estrategias de manejo actuales y alternativas en sistemas de producción agropecuarios que

permitan maximizar las áreas de bosque y los beneficios económicos (como descriptor global de la producción) a través de alternativas de manejo orientadas en intensificación sustentable (capítulo 4, Fig. 1.3, Tiftonell 2014). La figura 1.3 muestra el marco general de la tesis donde la escala más amplia considera el Paisaje Modificado por Actividades Humanas (PMH). Allí, las decisiones de las personas que lo habitan tienen efectos en la conservación de la selva remanente y sobre la producción agropecuaria (cuadros de líneas rojas, rayadas). El desafío último de esta tesis es integrar el componente de conservación y producción (cuadro inferior).

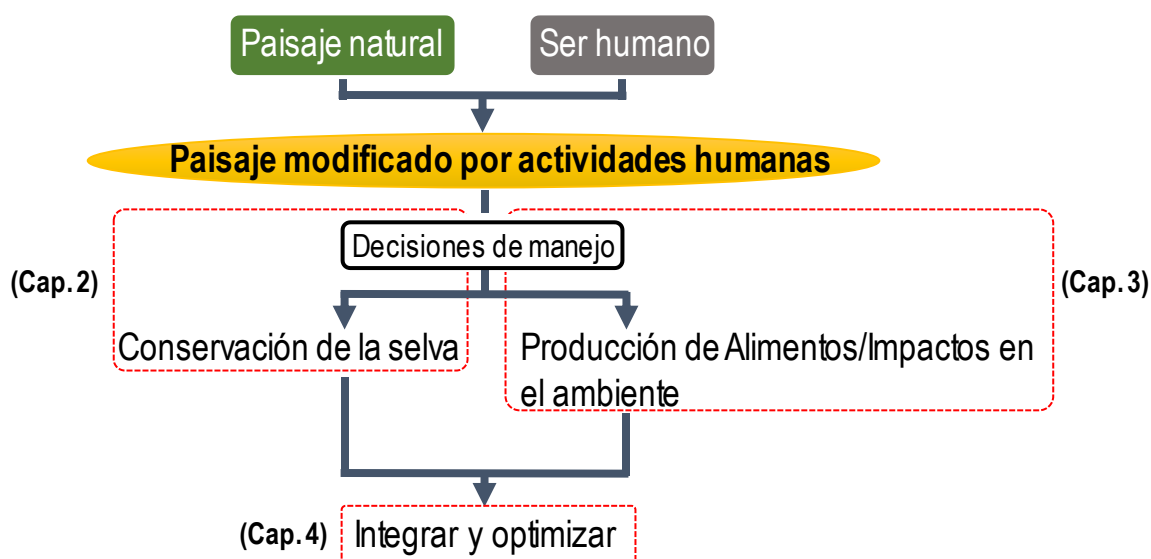


Figura 1.3: Marco conceptual integrador del proyecto de la investigación doctoral. En los paisajes modificados por actividades humanas, la conservación, la producción de alimentos y sus impactos en el ambiente están regulados por las decisiones de manejo de los tomadores de decisiones locales. Cuadros rojos indican los capítulos dos, tres y cuatro, correspondientes a los resultados.

1.3.1. Preguntas de investigación

La presente investigación doctoral abordó las siguientes preguntas fundamentales:

- 1 ¿Qué trayectorias de cambio experimentan la biodiversidad, las funciones del ecosistema y los servicios ecosistémicos en paisajes modificados por actividades humanas a medida que se reduce la cobertura de bosques y cambia la configuración del paisaje con el avance de la frontera agropecuaria?
- 2 ¿Qué factores biofísicos, productivos y socio-económicos impactan los rendimientos y sustentabilidad de los sistemas de producción de maíz dentro de los sistemas de producción agropecuarios?
- 3 ¿Cómo deberían conformarse o estructurarse los sistemas de producción agropecuarios dentro de los paisajes modificados por actividades humanas de manera que se maximicen la producción agropecuaria y las áreas de conservación de selvas, minimizando los impactos en el ambiente a través de criterios de intensificación sustentable?

Para responder la pregunta número uno, se plantea que los atributos de la estructura espacial del paisaje afectarán las respuestas de los atributos ecológicos de las selvas a la deforestación. Algunos atributos espaciales son composición (área y cantidad de parches de selvas) y configuración (número, densidad y complejidad de los parches de bosque en el paisaje, distancia entre los parches, densidad de borde de los parches y borde total de los parches, Fig. 1.3). Para la pregunta número dos, se plantea la hipótesis que los factores biofísicos (suelo, agua, temperatura y radiación), los factores socio-económicos y culturales

(origen, sexo, género, disponibilidad de tierra y apoyos financieros) pueden impactar en los factores agronómicos (nivel de insumos y decisiones de manejo) y en consecuencia el tipo de sistema de producción de maíz, su rendimiento y sustentabilidad (Fig. 1.3). Por último, para responder a la pregunta tres sobre balances entre conservación y producción, se utilizan modelos de simulación multi-objetivo de optimización de Pareto (Groot et al., 2012).

Los modelos de Pareto requieren datos de entrada que describen la composición de los sistemas de producción agropecuarios (cultivos, ganado, áreas de bosque, maquinaria, insumo), la descripción del funcionamiento (rendimientos, balance alimentario el ganado, circulación de estiércol y nutrientes, manejo de pasturas), la definición de las variables de manejo de la tierra, los límites del sistema y, por último, la definición de objetivos. Para el caso de la presente investigación, los objetivos se relacionaron con la maximización de las áreas de conservación de bosques y la maximización del beneficio económico de la producción a través de la optimización de estrategias de manejo basadas en intensificación sustentable. Es decir, se buscó maximizar la conservación maximizando también la auto-provisión de alimento para el ganado, maximizar la diversidad de cultivos y minimizar el uso de pesticidas y los costos variables (Fig. 1.3).

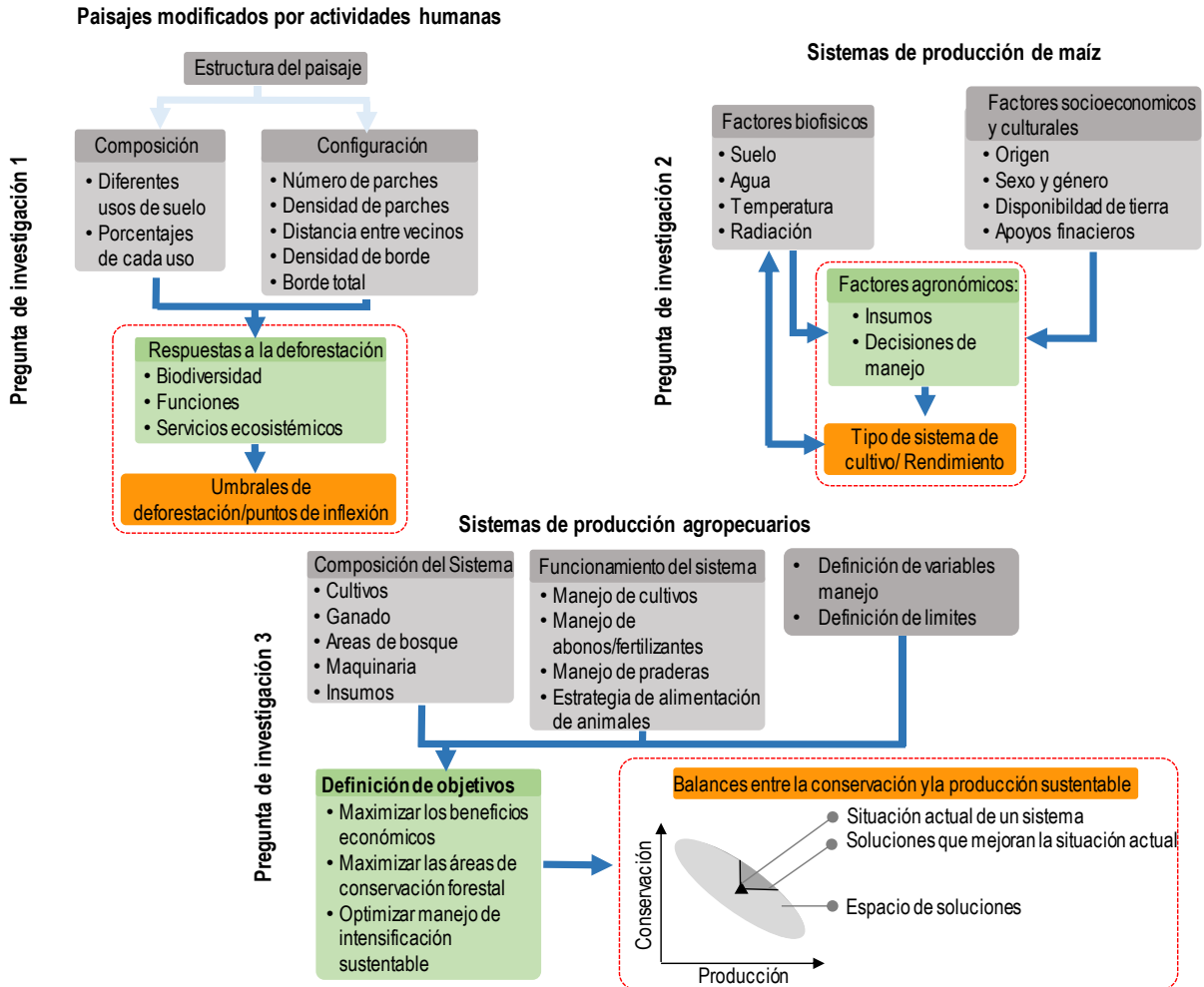


Figura 1.3. Modelos conceptuales desarrollados para responder las preguntas de investigación. La pregunta de investigación 1 se enmarca en paradigma de los “Paisajes modificados por actividades humanas” donde se espera que el gradiente de estructura del paisaje afecte la biodiversidad, funciones y servicios ecosistémicos de las selvas. La pregunta 2 se enmarca en los “sistemas de producción de maíz”, se espera que factores biofísicos, socioeconómicos y culturales determinen el tipo de sistema de cultivo de maíz y su rendimiento. Por último, la pregunta 3 se aborda en “los sistemas de producción agropecuarios”, se espera encontrar configuraciones de los sistemas de producción agropecuarios que permitan aumentar las áreas de bosque y la producción.

1.4. Objetivos

El objetivo general de esta tesis investigar qué composición y configuración de paisajes modificados por actividades humanas promueven balances positivos entre los componentes de conservación y producción agropecuaria en una región de elevada biodiversidad.

Objetivos particulares:

1. Describir las trayectorias de cambio que experimentan la B, las FE y los SE en paisajes que varían (en composición y configuración) a medida que se reduce la cobertura de bosques (de 100% hacia 0% de cobertura) con el avance de la frontera agropecuaria.
2. Describir y cuantificar cómo los factores biofísicos, productivos y socio-económicos impactan los rendimientos y sustentabilidad de los sistemas de producción de maíz.
3. Explorar qué composiciones del paisaje podrían mantener considerables niveles de B, EF y ES en las áreas de conservación y que a su vez maximicen la productividad de los sistemas de producción agropecuarios.

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Capítulo 2: Umbrales ecológicos críticos para la conservación de la selva tropical en paisajes modificados por humanos

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**Critical ecological thresholds for conservation of tropical
rainforest in Human Modified Landscapes**

Abstract

In the tropics, human modified landscapes (HMLs) emerge as potential areas where important levels of biodiversity, ecosystem functions, and services can be conserved. Yet, it is unknown which landscape structures may enable this goal. We studied how tree diversity (SD), aboveground biomass (AGB) and aboveground carbon storage (ACS) change across a gradient of forest-to-agriculture conversion process (0 to ~100%). We addressed following questions: i) How SD, AGB and ACS change with landscape composition and

configuration, as the forest-to-agriculture conversion advances? ii) Do such changes depend on the spatial scale of the landscapes, iii) Are there thresholds of forest habitat loss after which SD, AGB and ACS collapse? iv) If so, what explains such response? Changes in landscape composition, but not in configuration, explained the SD, ABG, ACS variability across the deforestation gradient. Percentage of forest cover was the best predictor of such variation, independently the landscape spatial scale. SD declined convexly, showing a critical collapse threshold, as forest loss advanced. AGB and ACS decreased exponentially with a 50% of reduction at ~30% of forest loss. We accord with previous studies targeted in other assemblages and forest trees variables that maintaining > 40% of forest is critical for tree diversity conservation. We broaden this estimation by alerting that ecosystem functions (e.g., AGB) and services (e.g., ACS) reduce with deforestation in a faster way than biodiversity. This exemplifies that different ecosystem attributes are affected differentially by deforestation, adding a strong challenge for conservation in HML.

Introduction

Forest cover worldwide has increased during the last three decades. However, this forest transition has resulted from a net loss of tropical forests and a net gain in forests from temperate and cold environments (Song et al., 2018). In the tropics however, remaining old-growth forest areas have been reduced at annual rates of 2-20% in the last two decades (Potapov et al., 2017). Because tropical forests harbor most of Earth's biodiversity, deforestation driven by human activities (mainly extensive agriculture, infrastructure

expansion, and wood extraction) is causing a high loss of biodiversity and its associated ecosystem functions and services (Barlow et al., 2018; Malhi et al., 2014).

Human modified landscapes (HMLs) may conserve forest habitats, and hence biodiversity, ecosystem functions and services (Melo et al., 2013). In the tropics, HMLs are composed of agricultural fields, roads, ecotourism areas, towns, remaining old-growth forest fragments, and patches of second-growth forests (Chazdon et al., 2009; Gardner et al., 2009). One major constraint for conservation in HMLs is the advance of the agriculture frontier, which causes the loss, fragmentation, and degradation of forest habitats (J. a Foley et al., 2005; Taubert et al., 2018).

The importance of forest fragments in HMLs for conservation has been broadly documented (Lenore Fahrig, 2017; Hernández-Ruedas et al., 2014). However, most studies have been conducted at the forest patch scale but not at the landscape level. The former approach (patch-scale design) focuses on how the surrounding landscape matrix affects the ecological properties (e.g., stand density, species diversity, biomass) of focal forest fragments, while the latter (landscape-scale design) explores how changes in the landscape structure affect ecological patterns and processes of entire landscapes (Fletcher & Fortin, 2018).

The assessments of the potential for conservation of HMLs require exploring the effects of forest-to-agriculture conversion on ecological guilds playing key roles in ecosystem functioning and services. Forest trees represent a key guild, as they are the main biomass producers and driver carbon, water, and nutrient cycles in the ecosystem (Hughes et al., 2000; Poorter et al., 2017). Furthermore, trees provide food, host and refuge for a

wide range of animals (I. M. Turner, 2001). Also, they are current or potential source of multiple forest products and services for society (Alamgir et al., 2016). For example, in only 4.5 ha of the Lacandon tropical rainforest, Navarrete-Segueda et al., (2017) recorded 94 tree species (57% of a total of 165) with one or more timber and non-timber forest products. Evaluating species diversity (SD), aboveground biomass (AGB) and aboveground carbon storage (ACS), related to forest trees, provides a good proxy to explore the potential of HMLs for conservation (Balvanera et al., 2005; Liang et al., 2016b).

The forest-to-agriculture conversion in HMLs is not homogeneous, landscape structure (composition and configuration) can strongly change as this process advances (Lenore Fahrig, 2017; Lenore Fahrig et al., 2011). Landscape composition (i.e., amount of forest habitat in the landscape), rather than landscape configuration (spatial arrangement of elements constituting the landscape), has been proposed as the best predictor for population genetic structure of tree species in modeled fragmented landscapes (N. D. Jackson & Fahrig, 2016). However, effects of landscape structure on tropical forest tree communities, have not yet been evaluated using a landscape-scale design. Moreover, little is known about how changes in landscape configuration (including variables such as number of forest patches, patch edge density, patch isolation, connectivity, and patch shape complexity) affect the conservation potential of whole HMLs (Lenore Fahrig, 2017). For example, reductions in patch size and increments in isolation and patch edge density in the landscape could reduce population densities, compromising the demographic or genetic viability of tree species (Alvarez-Buylla et al., 1996). Finally, the relationships between landscape structure and SD, AGB, and ACS may depend on the spatial scale of the analyzed

landscape (Suárez-Castro et al., 2018). To explore these potential interactions, the effects of landscape structure on SD, AGB and ACS at different scales will be evaluated.

HML encompassing a gradient of forest cover enables to test the “tipping point hypothesis” which says that a system can support an external disruption (deforestation) until some point where system’s rate of change is too high to recover the previous equilibrium and a new state arise (van Nes et al., 2016). Recent studies have shown that species diversity of terrestrial vertebrates and birds have tipping point (or thresholds) responses to forest cover loss (Banks-Leite et al., 2014; Ochoa-Quintero et al., 2015). Surprisingly, no marked thresholds were found when studying the tree communities in a forest cover gradient, identifying up to the family-level (Rocha-Santos et al., 2017).

We adopted a landscape-scale design to assess the effects of tropical rainforest-to-agriculture conversion on SD, AGB and ACS, and to identify HMLs structures with the potential for conservation. We assessed the following research questions: i) How does landscape composition and configuration affect SD, AGB, and ACS as the forest-to-agriculture conversion advances? ii) Do these effects depend on the spatial scale of the landscape? iii) Do SD, AGB and ACS trajectories exhibit deforestation thresholds after which these ecosystem properties collapse? iv) If so, what does explain such collapse? Finally, based on the results, we provide guidelines for landscape managers and policy makers to conciliate conservation and agricultural land-uses in HMLs.

Material and Methods

Study region

The study was conducted in the Marqués de Comillas region (MdC), Chiapas, Southern México (Fig. 1). This region covers an area of ~2,008 km². Mean annual precipitation is ca. 3000 mm and mean monthly temperature is 22°C (Martínez-Ramos et al., 2009). Vegetation structure and species composition is typical of tropical rainforest (Carabias et al. 2015; Navarrete-Segueda et al. 2018).

MdC has a long history of human presence starting with the Mayan civilization (more than 1,300 years ago) and the Lacandon group that lived in the region since about 500 years ago (de Vos, 1988). More recently (~1820-1950) there was a strong selective logging of highly valuable timber trees, for exportation to Europe (de Vos, 1988; de Vos & Marion, 2015). However, till 1970 the region remained covered mostly with old-growth forest (J Carabias et al., 2015). Since 1970 onwards, MdC was part of the land distribution program of the Mexican federal government and experienced a migration process of people from different states of Mexico (Chiapas, Guerrero, Jalisco, Michoacán, Oaxaca, Tabasco) and Guatemala (de Vos & Marion, 2015). Federal incentives, during the 70-80's promoted cattle ranching pastures, which led to a fast deforestation (Carabias et al. 2015). Since then, the most common land use practice is cattle ranching (Zermeño-Hernández et al., 2015). Currently, ~70% of the region is covered by cattle pastures, crop fields, commercial plantations, second-growth forest patches, and human settlements (Zermeño-Hernández et al., 2016).

Study system

Landscape units (LUs). We used Sentinel-2 satellite imagery (10-m, <https://sentinels.copernicus.eu/web/sentinel/home>) from MdC to identify different land

uses. First, we developed an object-based classification of the whole region, based on the texture variance of the red and infrared bands and considering a spectral resolution of 2 μm (Willhauck, 2000). This technique has been employed to distinguish different vegetation types and successional stages (M. A. Castillo-Santiago et al., 2010). We selected two images (to totally cover the MdC region) from February 22nd, 2017, filtering those with less than 10% of cover clouds. The region is almost plain, and we did not filter nor correct topographic variability. Also, we did not consider changes in reflectance due to the seasonality because tropical rainforest is evergreen even in the dry seasons.

Using the resulted classification map, we located and recorded UTM coordinates of twenty-nine LUs of 1-km² with different percentage of forest cover, from which we selected twenty (Fig. 1). These landscape units absorbed the spatial-soil effects on response variables. We made sure that landscapes units with high, medium, and low coverage were present in the two main geomorphological units occurring in the study region (Navarrete-Segueda et al. 2018). We considered an extent of 1-km² because at this scale human disturbances (e.g. deforestation, fires), climate fluctuations, and the spread of pests or diseases are well represented (Delcourt et al., 1983). Also, successional changes in the structure and composition of trees can be well described (M. G. Turner & Gardner, 2015). LUs differed in the percentage of forest cover encompassing the whole range (~0 to 100%) of deforestation (Appendix S1). This gradient can be compared to a chronosequence. This approach substitutes time for space. Although, this substitution has the limitation of assuming that all sites included have the same land use history and similar initial environmental conditions, it has the advantage of providing a way to make inferences about

patterns and processes occurring during long time periods (tens or hundreds of years; Foster and Tilman 1999; Walker et al. 2010).

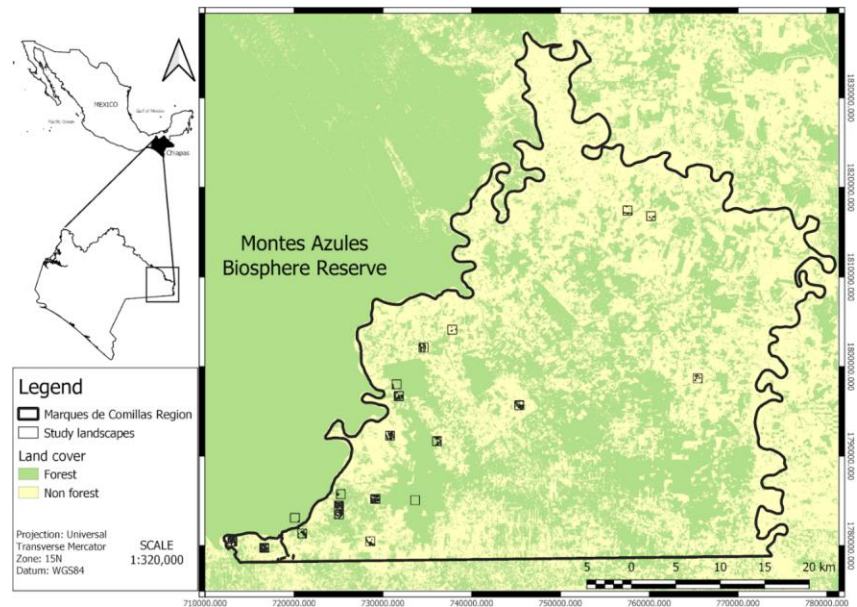


Figure 1. Map of location of the studied landscape units in the Marqués de Comillas region, Southeastern México. Each square represents a landscape unit of 1km².

In each LU we established a grid of 100 equidistant points and randomly choose thirty, and recorded their geographic coordinates (QGIS 2009). In the field, with a GPS, we located each point, which was used to establish a circular sampling area of 15 m radius (subplot, 706.9 m²). We established thirty subplots (2.17 ha) per LU (600 subplots across the 20 LUs) to cover evenly the different land cover types in each landscape. In each subplot, all trees with a diameter at breast height (DBH) ≥ 10 cm were recorded. We measured DBH, stem height and determined taxonomic identity. For trees with buttresses, we measured DBH above these structures. Samples of unidentified specimens were taken

for further identification in herbaria. The land use type (old-growth forest, secondary forest, pastures, and annual crops) for each subplot was also recorded.

Data analysis

Landscape structure (explanatory variables).

With land-use data obtained in the field, we performed a landscape photo-interpretation for each LU (McKeown, 1984). We used PLANETSCOPE (www.planet.com) imagery of 3-m resolution (between the dates February 21 - 23, 2017) with less than 10% of cover clouds. Also, we used the previous object-based classification (Appendices S2 A, S2 B and S2 C). This procedure allowed us to have an accurate description of the spatial distribution of the different land uses validated with field data and avoiding shadow spots (created by the forest-pasture height contrast in the object-based classification, Appendix S2D).

After the photointerpretation, we conducted an analysis of the landscape structure of each LU, using 17 landscape metrics that encompassed all possible indicators of landscape composition and configuration of the landscape (Appendix S3). We selected forest cover area and percentage of forest cover as landscape composition variables. Also, we selected eight landscape configuration metrics associated to patch size, edge, shape, isolation, and fragmentation. These metrics describe the shape and the spatial distribution of the forest patches in each LU (Appendix S3) and are associated with changes in vegetation diversity and aboveground biomass in fragmented tropical rainforests (Hernández-Ruedas et al., 2014; William F. Laurance et al., 2007). Landscape metric effects can differ between patch- and landscape-centered measures (Wang et al., 2014). Therefore, to detect possible weighted measurements we included, standard deviation (a patch-centered measure of

heterogeneity) and area-weighted mean (a landscape-centered measure) in some metrics of interest (Appendix S3).

To obtain metrics we used FRAGSTATv4 software (McGarigal et al., 2012). This software uses a raster layer (each LU) as entry and returns values of landscape metric for all uses (we considered the forest cover use, Appendix S3). Also, we quantified all these metrics by increasing LUs areas: 1, 1.5, 2, 2.5 and 3 km². These values were used in the “scale of the effect” analysis (see below, “*scale of effects*”).

We used a principal component analysis (PCA, Abdi and Williams, 2010) to identify metrics that explained most variation among the twenty LUs (Appendix S4). PCA axis-1 and axis-2 explained 48.1% and 18.3% of total variation, respectively (Appendix S4). Axis-1 grouped metrics related to forest amount. We selected the percentage of forest cover (PLAND) because it was highly correlated to axis-1 (Appendixes S4 and S5) and it was the fourth variable contributing the more to the total variation explained by axis-1 (Appendixes S6). The axis-2 grouped metrics related to the patch form complexity (i.e., ED, TE and AREA_SD) and negatively to the patch isolation (i.e. Euclidean nearest neighbor mean distance, ENN_MN; Appendix S5 and S6). From axis-2, we selected edge density (ED), which most contributed to total variation in axis-2 (Appendix S7), and ENN_MN as it showed the highest negative correlation with this axis (Appendixes S4 and S5).

Tree community (response variables). We quantified SD, AGB and ACS for each landscape unit aggregating the data from the 30 subplots. To describe SD we choose “Hill” numbers (Chao et al., 2014), which are used to estimate the number of species (i.e., species density;

$q = 0$), the number of common species (equivalent to the exponential of Shannon-Wiener diversity index; $q = 1$), and the effective number of dominant species (equivalent to the inverse of the Simpson's diversity index; $q = 2$). We verified the sampling completeness in each LU following Chao and Shen (2010). Eighteen of the 20 LUs exhibited completeness over 75%, and only two were below this level (Nueva Chihuahua 50% and Benemerito-1, 62%). Therefore, we did not calculate rarefaction neither extrapolations and considered the species density as the best estimator of tree species richness.

We quantified AGB of all sampled trees across LUs. For this, we estimated biomass of each individual tree using the allometric equation provided by Chave et al. (2014):

$$AGB_i = 0.0673 \times (\rho D^2 H)^{0.976} \quad (1)$$

Here, AGB_i is the aboveground biomass of the i tree, ρ is the mean wood density for the i tree, D and H are the diameter (cm) at 1.3 m aboveground and the height (m) of the tree, respectively. Mean wood density was obtained from data *in-situ*, literature, or a global database (Chave et al., 2014; Poorter et al., 2017). We estimated AGB per LU by summing up AGB_i of all trees recorded in the 30 subplots for each LU.

We estimated aboveground tree carbon storage (ACS) considering that 47.4% of AGB in tropical rainforest trees is carbon (Martin & Thomas, 2011).

Landscape structure effects on SD, AGB, and ACS

To assess how landscape composition and configuration affected SD, AGB, and ACS we used general linear models (LMs). In the models, we considered Hill numbers (q_0 , q_1 and q_2), AGB and ACS as response variables, and the selected landscape structure metrics, as

explanatory variables. Also, we included a quadratic term in the PLAND, to include possible curvilinear effects. The GLMs had the following equation:

$$\text{Response} \sim \text{PLAND} + \text{PLAND}^2 + \text{ED} + \text{ENN_MN} \quad (2)$$

We considered the percentage of total deviance (equivalent to R^2) explained for each independent variable as a criterion of the strength of their effect on SD, AGB, and ACS. To relate Hill numbers and PLAND, we used Michaelis-Menten since trajectories of change were non-linear. For SD models we set the maximum diversity value observed in the 100% old-growth LU as a model constraint. Finally, we used segmented regression analysis to detect possible thresholds in the SD, AGB and ACS trajectories, as described in Banks-Leite et al. (2014).

The scale of the effects

We tested whether landscape structure extent affected SD, AGB, and ACS by increasing the spatial scale of the LUs, adapting to our design the protocol of Miguet et al. (2016). We quantified landscape metrics (PLAND, ED and EEN_MN) for LUs of increasing area: 1, 1.5, 2, 2.5 and 3 km². For each LU scale, we considered the metrics as independent variables and SD, AGB and ACS values recorded in the 1-km² LU as response variables. Using the equation 2, for each scale, we obtained the model R^2 and the proportion of total deviance. Finally, we regressed R^2 against LUs extent (Appendixes S8 and S9).

Explaining SD, AGB, and ACS relationships

We assessed if changes in population density and biomass of individual species determined the trajectories of change in SD, AGB, and ACS. We gathered the twenty LUs in four categories of percentage of forest cover: very low (< 25%), low (26-50%), moderate (50-75%), and high (> 75%). For each category, we plotted the relative species contribution to total AGB as a function of their relative abundance (Y and X axes in \log_{10} scale). We defined boundaries based on orders of magnitude intervals to distinguish species with low (< 1% of total individuals), intermediate, or large (>10%) contribution to total AGB, and those with low (<1%), intermediate, or high (>10%) contribution to total abundance. Using these boundaries, we detected species that highly contributed to AGB in comparison to their relative abundance (Balvanera et al., 2005). In addition, we constructed similar graphs but using the absolute values of AGB and population density of each species (Appendix S11).

Results

The landscape structure effects on SD, AGB, and ACS

PLAND (or the quadratic term) was the best predictor of SD, AGB and ACS. ENN_MN only affected the number of dominant species (Table 1). This result was maintained when we considered LUs of increasing scale. In all cases, R^2 of the models remained quite constant across scales (Appendixes S8 and S9). At all spatial scales, PLAND or PLAND² retained the highest proportion of total deviance (Appendix S10).

Table 1. Effects of landscape composition (percentage of forest cover, PLAND) and configuration (edge density of forest patches, ED and inter forest patch connectivity, ENN_MN) metrics on tree SD (species density, number of common species, and number of

dominant species), aboveground biomass (AGB), and aboveground carbon storage (ACS) across the forest-to-agriculture conversion in Marqués de Comillas, Southern Mexico. In all cases, linear models were fitted with landscape metrics as independent regressors. The significance of the parameters (Par) and the proportion of the deviance (R^2) explained of each independent variable are shown. * = $p < 0.05$; *** = $p < 0.001$.

Response
variable

Source	Species Richness		Number of common species		Number of dominant species		AGB		ACS	
	Par	R^2	Par	R^2	Par	R^2	Par	R^2	Par	R^2
Intercept	-1.11		-1.09		1.30		-24.9		-11.8	
PLAND	1.56 ***	0.96	0.80***	0.89	0.06***	0.70				
PLAND ²	0.00	0.00	-0.01	0.03	-0.00*	0.12	0.09***	0.91	0.04***	0.91
ED	0.05	0.00	0.02	0.00	0.01	0.04	0.84	0.01	0.39	0.01
ENN_MN	0.05	0.01	0.01	0.00	0.00*	0.06	0.25	0.01	0.12	0.01
Residuals		0.03		0.08		0.08		0.07		0.07
R^2	0.97		0.92		0.92		0.93		0.93	
R^2_{adjusted}	0.95		0.87		0.88		0.90		0.90	

Trajectories of tree SD, AGB and ACS with the forest cover loss

Species density decreased convexly as the percentage of forest cover was reduced in the landscape (Fig. 2A). The maximum species value was 131, found in 100% forest cover LU.

When forest cover reduced beyond 60% species density and the number of dominant species declined rapidly to zero (Fig. 2A and C). Common species presented this sharp decline beyond 80% of forest cover loss (Fig. 2B).

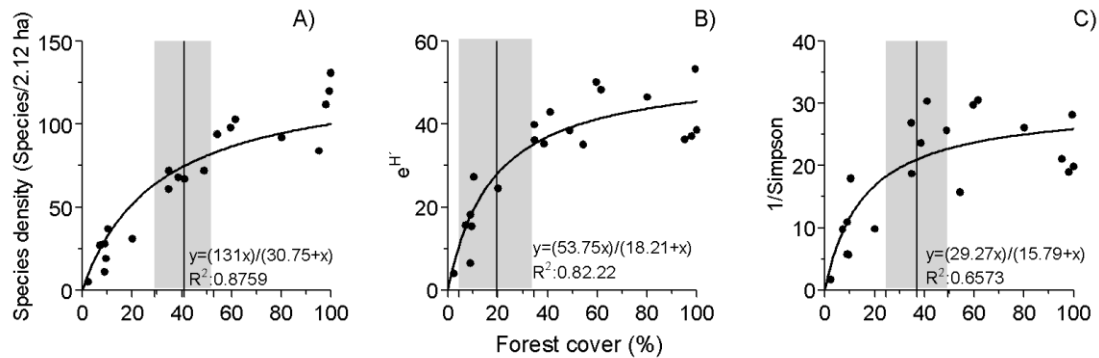


Figure 2. Trajectories of change in tree species diversity as the percentage of forest cover (PLAND) reduces in landscape units in Marqués de Comillas, Southeastern Mexico. A) Species density, i.e., number of species in the sampling area (2.12 ha) per landscape unit. B) Number of common species calculated as $\exp(H')$. C) Number of dominant species calculated as the inverse of the Simpson' index. Data points were adjusted to Michaelis Menten models (each point correspond to one landscape unit) using the least squares method. For each graph, the adjusted model and R^2 values are shown. Vertical lines indicate thresholds of forest cover loss beyond which the slope of the response exhibited a sharp change. The grey bars indicate 90% confidence intervals around threshold.

AGB and ACS were highly sensitive to the loss of forest cover in the landscapes. Both variables decreased exponentially as soon as percentage of forest cover started to decrease (Fig. 3A). This rapid decline was partially explained by a linear reduction of the number of trees (Fig. 3B) but also by a decrease in the size of individual trees as the forest cover reduced in the landscape (Fig. 3C).

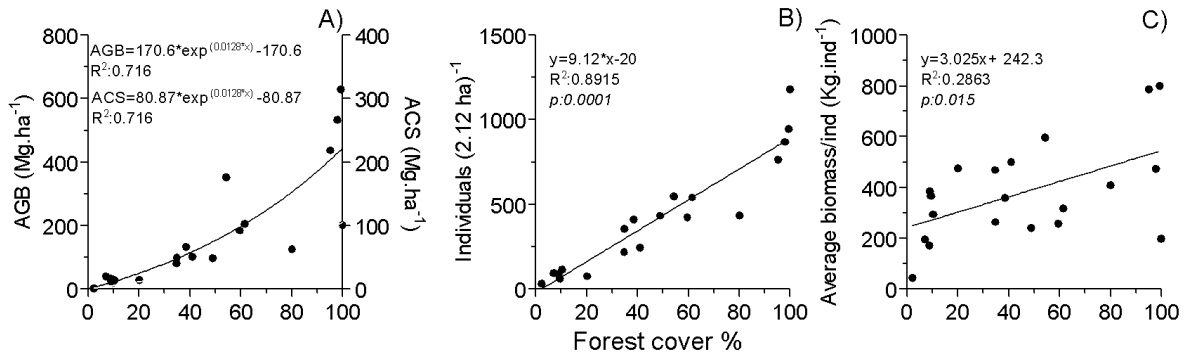


Figure 3. Changes in biomass, carbon storage, and density of tree assemblages as percentage of forest cover reduce in the landscape at Marqués de Comillas, Southeastern Mexico. A) Aboveground biomass (AGB, left axis) and aboveground carbon storage (ACS, right axis), as a function of percentage of forest cover. B) Tree density, and C) mean tree biomass as function of percentage forest cover. For each graph, the adjusted model and the proportion of explained deviance (R^2 values) are shown. Note that in (A) models were constructed independently for AGB and ACS, but only one regression curve is drawn because ACS is a fraction of AGB over all values in the X's axis.

Explaining trajectories of reduction in SD and AGB

Changes in SD and AGB produced by forest reduction in LUs were not independent. Many rare species (relative abundance < 1%), especially those with high relative contribution to AGB (> 1% to 10% of total biomass), were locally extinct (e.g. *Luehea speciosa*, *Ceiba pentandra*, and *Vatairea lundellii*, among others; Fig. 4A, see dark green labels). The number of such rare species decreased progressively as the forest cover declined in the landscapes, from 28 in LUs with 100% forest cover to 2-6 in LUs with very low forest cover (Fig. 4 A-1D). Also, LUs with high forest cover showed a much wider range of population densities (1 to 151 trees/2.12 ha) and AGB values (0.009 to 226 Mg/2.12 ha) than LUs with very low forest cover (1 to 24 trees/2.12 ha and 0.007 to 32.7 Mg/2.12 ha,

respectively; Appendix S11D). Furthermore, while in LUs with moderate to high forest cover between 38 and 48% of the species showed population densities of 8-256 trees/2.12 ha, in LUs with very low forest cover 75% of the species showed very low population densities (1-4 trees/2.12 ha; Appendix S12).

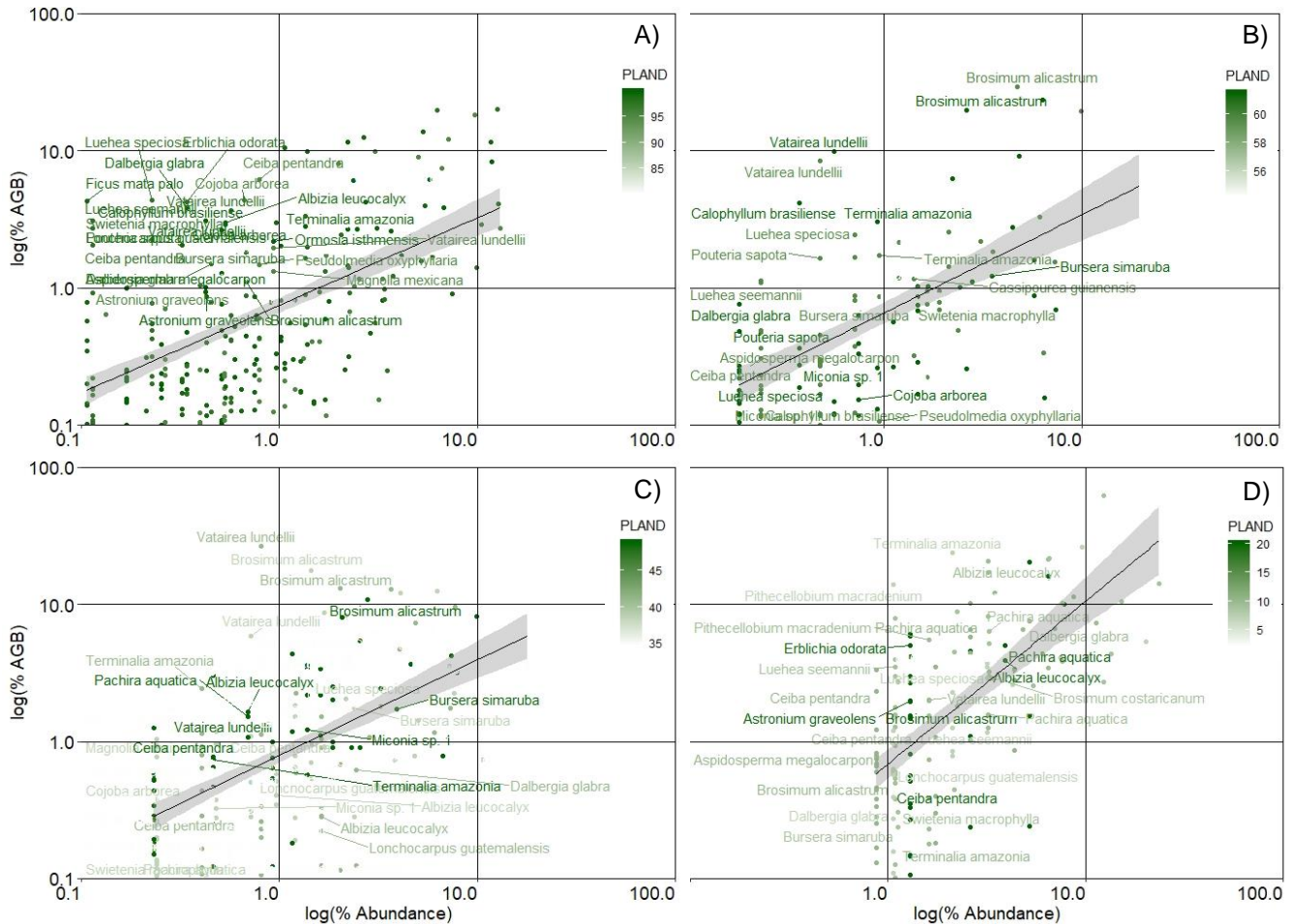


Figure 4. Relationship between relative AGB contribution and relative abundance for single tree species in landscape units (LU) with increasing levels of forest loss at Marqués de Comillas, Southeastern Mexico. X and Y-axes in \log_{10} scale. Graphs correspond to LU categories with: (A) 75-100%, (B) 50-75%, (C) 25-50%, and (D) 0-25% forest cover. Rare species (relative abundance < 1%) that importantly contribute to total biomass (>1% to

10% AGB) are labeled. Species recorded in more than one LU in a given category can be labeled more than once.

Discussion

There is a growing theoretical literature focusing on the conservation potential of HMLs (Arroyo-Rodríguez et al., 2015; Chazdon et al., 2009). However, conservation in HMLs requires developing accurate baseline information on deforestation thresholds driving to ecosystem collapse. Thus, it is necessary to determine how much forest cover is required to avoid such thresholds, and also, to analyze how these forest areas are interrelated with other land uses in the matrix (Gardner et al., 2009; Sodhi et al., 2010).

For tree species we found that landscapes with forest cover greater than 50% ($40 \pm 10\%$, Fig.2), independently of landscape configuration, exhibited species diversity levels comparable to landscapes fully covered. However, the AGB and ACS showed an exponential reduction as soon as deforestation began. These results were consistent even when the spatial scale of the LUs increased from 1-km² up to 3-km². The decline in SD, AGB and ACS resulted from a progressive reduction in population density in most species (Fig 3B) and from the loss of rare species with an extreme contribution to forest biomass (Fig 3C and 4).

Changes in landscape structure and its effects SD, AGB and ACS

Fahrig (2017) proposed that landscape composition and configuration should be separately analyzed because they might have different effects on ecosystem attributes. Our results showed that landscape configuration did not affected SD, AGB nor ACS, while landscape

composition (percentage of forest cover, PLAND) was the best predictor for these ecosystem variables. The effects of changes in PLAND on adult tree species diversity and biomass would importantly depend on the abundance and distribution patterns of the species established before deforestation. This is because changes in the population dynamics of large trees occur at the scale of decades (Condit et al., 1992). When an old-growth forest landscape is converted to agriculture this slow dynamic is drastically disrupted. On one hand, in active fields the use of fire, agrochemicals, machinery or cattle trampling strongly limit the recruitment of forest tree species (Martínez-Ramos et al., 2016). On the other hand, severe agriculture regimes impede tree regeneration in abandoned fields (Zermeño-Hernández et al., 2015). Hence, in landscapes under recent conversion to agriculture (as in our case), tree species diversity and biomass will critically depend on the abundance, distribution, and sizes of trees in the old-growth forest remnants.

Trajectories of change in SD, AGB, and ACS and deforestation thresholds

Tree species diversity decreased convexly with the forest cover loss while AGB and ACS did it exponentially. Beyond ~60% of deforestation (Fig. 2A, B) species diversity reduced very rapidly. In a similar study in the Brazilian Atlantic rainforest but determining taxonomic families of individual adult trees, no clear thresholds were found neither in tree community richness nor abundance (Rocha-Santos et al., 2017). The taxonomic species determination in our study may have improved the community composition description dynamic as the forest-to-agriculture process increased. Moreover, in agreement with our results, the same researcher found that forest structure responses (canopy openness, basal area, tree diameter and stratification) had a threshold at 40% of forest cover (Rocha-Santos

et al., 2016). The 40% (± 10) threshold was higher than that found in a Brazilian Atlantic rainforest (30%) for different groups of vertebrates (Banks-Leite et al., 2014), suggesting that tree communities are more sensitive to deforestation. Banks-Leite et al. (2014) also speculated that ecological functions of vertebrates might change before and after the deforestation threshold. Accordingly, we found that AGB and ACS were much more affected than SD. This implies that diversity cannot be the single criterion and it is important to regard key ecosystem functions and services linked to biodiversity to assess the conservation potential of HMLs (Balvanera et al., 2016).

Relationships between species diversity and ecosystem services with loss of forest cover

The fast reduction in AGB and ACS with the forest-to-agriculture conversion was explained by a progressive decrease in species population density, size of trees, and with a progressive loss of rare species with high contributions to total landscape biomass. Our results concur with Poorter et al. (2017) who showed that as tree species diversity increases more potential exists for stocking carbon, a key ecosystem service for climate regulating (Malhi & Grace, 2000). Previously, Balvanera et al. (2005) pointed out this diversity-carbon stock relationship for tropical rainforests. Our results reinforce this relationship, highlighting the importance of conserving tree species diversity in HMLs for programs such as REDD+.

The tree species loss may alter key ecosystem processes and important ecosystem services, because different plant species contribute to a wide spectrum of traits linked to several ecosystem functions (Cardinale et al., 2012). Supporting and regulating ecosystem services such as soil formation, nutrient and water cycling, water regulation, primary

productivity, C storage, air quality regulation, erosion regulation, nutrient regulation, and hurricanes protection have been shown to be in higher supply in the old-growth forest than in secondary forest or agricultural fields (Alamgir et al., 2016; Ferraz et al., 2014). Hence, the exponential decline in AGB and ACS, may have direct and negative consequences in the supply of these ecosystem services and on the human wellbeing.

Limits of the experiment and implications

When assuming a spatial deforestation gradient (our case), temporal and spatial dimensions may be interacting. Spatial effects could affect the temporal population dynamics of trees occurring, for example, local extinction because of endogamy or genetic drift (Alvarez-Buylla et al., 1996; Hardy et al., 2006). In our study, the deforestation process was fast (~40 years). On the other hand, trees become adult after 20-30 years (Condit et al., 1995). Thus, the majority of trees, which could be influenced by deforestation-temporal dynamics, were still young and weren't included in our target adult trees group. Because of this, we attributed our results only to spatial and not to temporal effects. Thus, we considered that adult trees biodiversity responses were constant in the deforestation period (~40 years) and changes were only due to spatial effects (landscape structure).

Finally, we suggest that long-term samplings describing species population dynamic in experiments of spatial gradients (like this), could disentangle spatial, temporal as well as the interaction effects on biodiversity responses.

Implications for conservation in HMLs

As shown here, the conservation of tree SD, AGB and ACS in tropical HMLs require the maintenance of important levels of forest cover. Because AGB and ACS were more sensitive to deforestation than SD, the potential for conservation of HMLs demand higher levels than those required to preserve SD, i.e. > 50% forest cover. We highlight that the percentage of forest cover in the landscape is more important than its spatial arrangement at least for the configurational gradient present in this study (see effects of fragmentation on tree populations at patch level in Laurance et al., 2007, 1998). This opens the possibilities for farmers to design agricultural production systems considering forest patches as a tool beneficial for production. Preventing soil erosion in high slopes areas with forest cover or leaving streams with riparian vegetation to maintain the water levels are examples of these synergies (Grimaldi et al., 2014). Finally, we highlight the importance of conserving old-growth forest patches with key species that highly contribute to ecosystem function and services. Governmental public policies, and global, regional, and local community initiatives should include species protection programs and education to the inhabitants about the importance of these species for these ecosystems.

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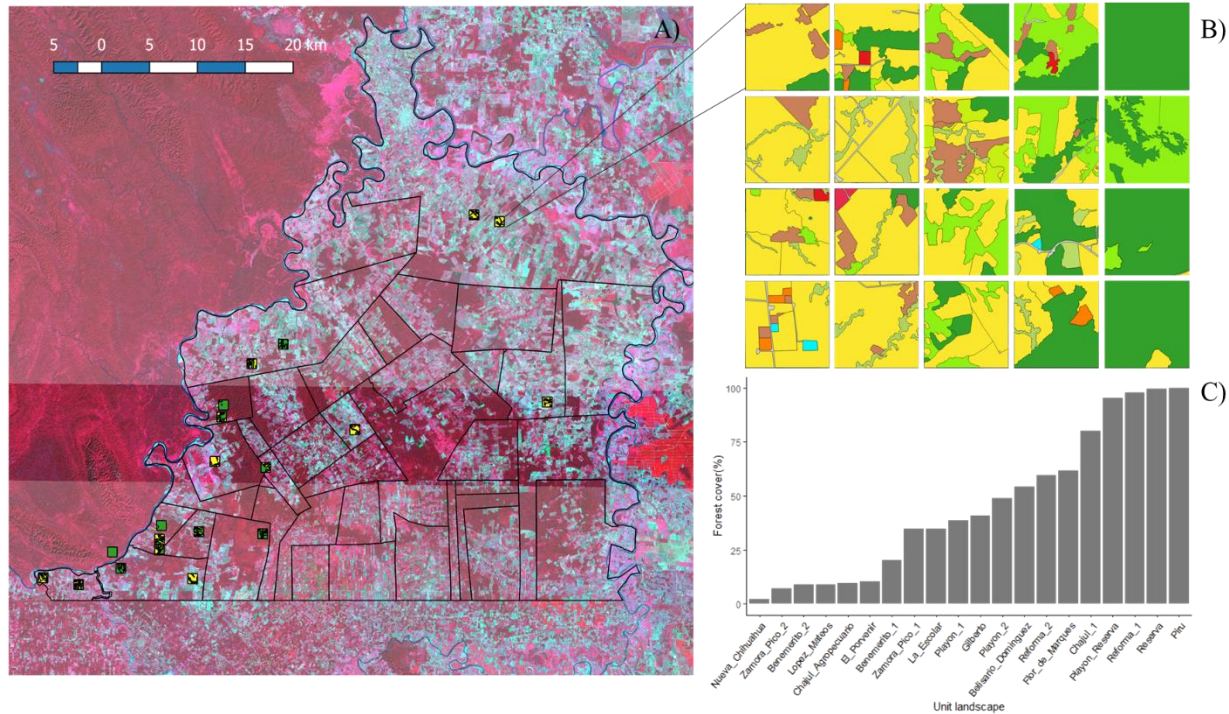
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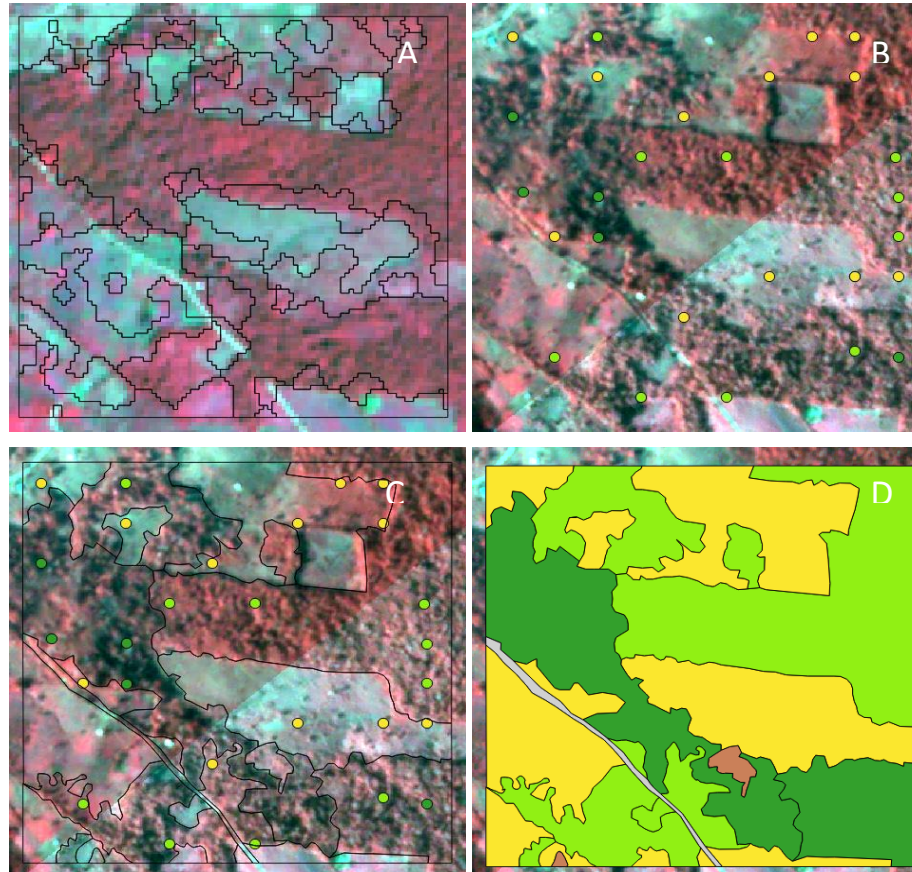
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2.1 Capítulo 2: Figuras complementarias

Appendices (supporting information)



Appendix S1: A) Distribution of twenty studied landscape units (1 x 1 km) established across different ejidos (villages, polygons defined by contour lines) in Marqués de Comillas, Southern Mexico. A) Sentinel images, 2017 (10-m); the different contrast colours are obtained by changing band combination to “false green” (www.visibleearth.nasa.gov). B) The twenty landscape units with different percentage of primary forest (green), second-growth forest (light green), riparian forest (slashed green); yellow, brown, orange, red and light blue correspond to different agricultural uses: to cattle production, abandoned pastures, maize crops, palm oil plantations, and “mahogany tree” afforestation, respectively. C) Variation of forest cover percentage (primary forest + secondary forest + riparian forest) across the twenty landscape units.

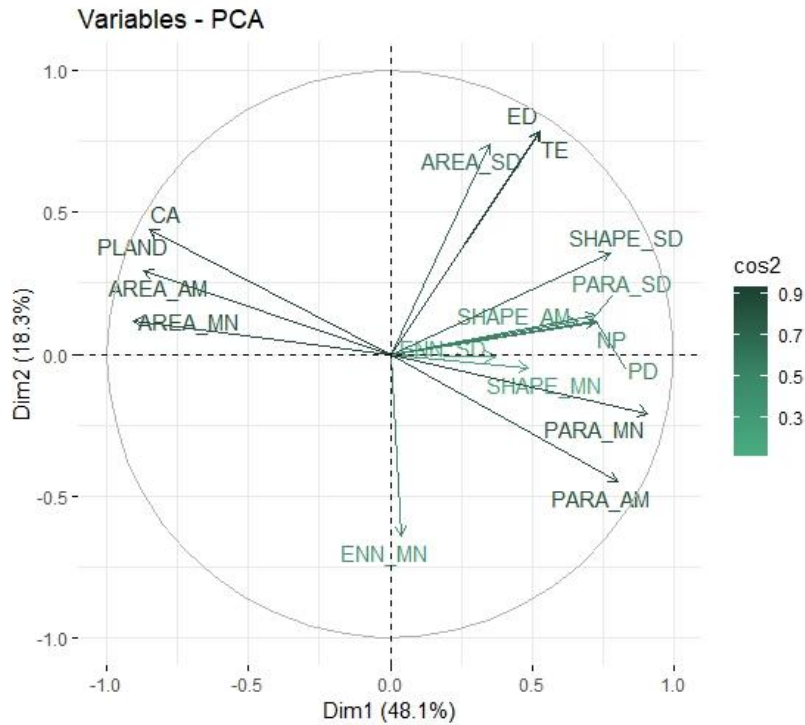


Appendix S2. Example of the photointerpretation applied for obtaining landscape uses in each landscape unit in Marqués de Comillas region, Chiapas, Mexico. A) Example of one landscape unit cropped from Sentinel-2 images (10m) and the object-based classification. B) Planet-scope image (3-m resolution) from the same area. Each dot represents one subplot (15-m radius; $n = 30$) and its colour indicates the land use cover type (dark green, old-growth forest; light green, secondary forest; yellow, pastures and brown, abandoned pastures). C) Photointerpretation drawing supported by A) and B) information. D) Final photointerpretation used to the landscape structure analysis. This procedure repeated for twenty landscape units.

Appendix S3. Metrics of landscape composition and configuration calculated for each of the 20 landscape units (LU) studied at Marqués de Comillas, Chiapas, Southern Mexico. In these values, forest cover included old-growth, second-growth and riparian forests. In the column “Site” the name of the LU is provided. Landscape composition metrics: CA = area amount (hectares), PLAND = percentage of forest cover respect to the total area of each LU. Landscape configuration metrics: NP = number of patches, PD = density of patches, TE = total length of patch edges (m), DE = edge density, AREA_MN = mean area of the patch, AREA_AM = mean-weighted of patch area, AREA_SD = standard deviation of AREA_AM, SHAPE_MN = index of mean form (SHAPE, calculates an index of complexity of the patch with respect to a standard), SHAPE_AM = index of mean-weighted form, PARA_MN = perimeter- mean patch area relationship, PARA_AM = perimeter- mean-weighted patch area relationship, PARA_SD = standard deviation of PARA_MN, ENN_MN = Euclidean nearest neighbour mean distance, and ENN_SD = standard deviation of ENN_MN.

Site	CA	PLAND	NP	PD	TE	ED	AREA_MN	AREA_AM	AREA_SD	SHAPE_MN	SHAPE_AM	SHAPE_SD	PARA_MN	PARA_AM	PARA_SD	ENN_MN	ENN_SD
Belisario Dominguez	54.7	54.3	1	1.0	7257.0	72.1	54.7	54.7	0.0	2.8	2.8	0.0	151.1	151.1	0.0	NA	NA
Benemerito 1	20.3	20.1	5	5.0	8574.0	84.9	4.1	9.9	4.9	2.3	2.6	0.4	625.2	421.4	229.7	14.1	4.4
Benemerito 2	9.0	8.9	1	1.0	6864.0	68.0	9.0	9.0	0.0	5.7	5.7	0.0	761.0	761.0	0.0	NA	NA
Chajul 1	80.7	80.1	1	1.0	9036.0	89.7	80.7	80.7	0.0	2.7	2.7	0.0	119.9	119.9	0.0	NA	NA
Chajul Agropecuario	9.6	9.6	4	4.0	7584.0	75.3	2.4	5.4	2.7	2.9	4.2	1.2	1266.5	788.3	613.4	121.3	146.4
El Porvenir	10.9	10.4	1	1.0	4923.0	46.9	10.9	10.9	0.0	4.0	4.0	0.0	481.5	481.5	0.0	NA	NA
Flor de Marques	62.0	61.5	2	2.0	11859.0	117.8	31.0	50.4	24.5	3.0	3.3	0.4	301.6	208.2	118.0	8.5	0.0
Gilberto	41.2	41.0	3	3.0	11982.0	119.3	13.7	38.1	18.3	2.9	4.4	1.2	832.4	313.1	432.9	92.1	107.4
La	35.0	34.9	3	3.0	9015.0	89.8	11.7	21.0	10.5	2.4	2.8	0.5	353.2	276.5	109.1	80.7	12.2

Escolar																	
Lopez																	
Mateos	9.2	9.1	2	2.0	1545.0	15.3	4.6	7.7	3.8	1.4	1.3	0.1	408.2	223.7	224.9	280.1	0.0
Nueva																	
Chihuahua	2.3	2.3	2	2.0	1515.0	15.0	1.1	1.7	0.8	1.9	2.0	0.2	895.1	665.9	317.0	61.8	0.0
Piru	100.0	99.9	1	1.0	1490.9	14.9	100.0	100.0	0.0	1.0	1.0	0.0	40.7	40.7	0.0	NA	NA
Playon 1	39.0	38.6	4	4.0	10944.0	108.4	9.7	29.4	13.8	2.1	3.4	1.0	844.6	281.6	818.9	46.1	21.5
Playon 2	49.9	49.0	3	2.9	8778.0	86.1	16.6	17.2	3.0	2.0	1.9	0.4	197.9	187.4	59.1	48.5	34.6
Playon																	
Reserva	95.6	95.2	1	1.0	2526.0	25.2	95.6	95.6	0.0	1.2	1.2	0.0	47.3	47.3	0.0	NA	NA
Reforma 1	98.9	97.9	1	1.0	3996.0	39.6	98.9	98.9	0.0	1.0	1.0	0.0	40.4	40.4	0.0	NA	NA
Reforma 2	60.2	59.6	4	4.0	8982.0	88.9	15.1	36.5	17.9	1.6	2.0	0.4	471.8	149.1	410.9	31.8	31.9
Reserva	99.8	99.4	1	1.0	1998.0	19.9	99.8	99.8	0.0	1.0	1.0	0.0	40.0	40.0	0.0	NA	NA
Zamora																	
Pico 1	35.1	34.7	4	4.0	8412.0	83.3	8.8	13.6	6.5	1.7	2.0	0.4	268.3	239.7	43.3	21.5	17.5
Zamora																	
Pico 2	7.2	7.1	8	7.9	5910.0	58.5	0.9	1.7	0.9	2.0	2.2	0.9	1184.6	822.0	529.0	134.3	95.7

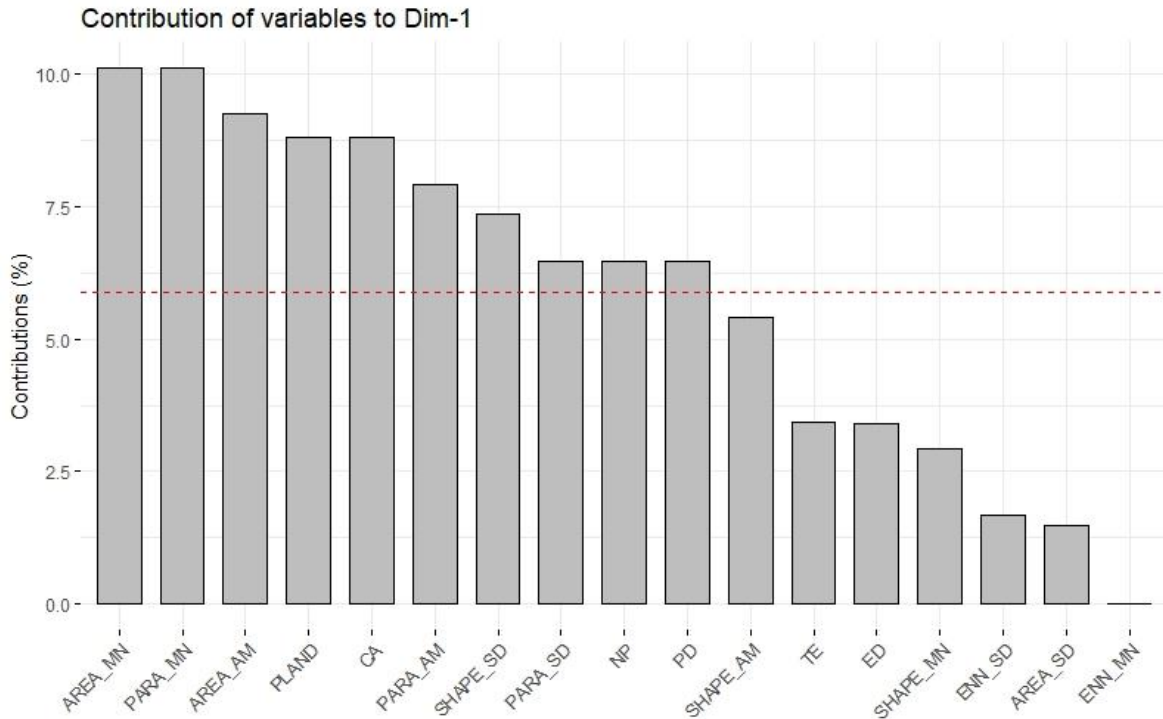


Appendix S4: Results of the principal component analysis (PCA). Results are shown as a circle of pairwise correlations (*sensu* McGarigal et al. 2012) between each one of 17 metrics of landscape structure and axis-1 and axis-2 of the PCA. Each arrow represents a metric of the landscape structure. Metrics: CA = area amount (in hectares); PLAND = percentage of forest cover respect to the total area of a landscape unit (1 km²); NP = number of patches; PD = density of patches; TE = total length of patch edges (m); DE = edge density; AREA_MN = area mean of the patch size; AREA_AM = mean-weighted area of the patch size; AREA_SD = standard deviation of AREA_AM; SHAPE_MN = index of mean form (SHAPE, calculates an index of complexity of the patch with respect to a standard); SHAPE_AM = index of mean-weighted form; PARA_MN = perimeter-area mean patch relationship; PARA_AM = perimeter-area mean-weighted patch relationship; PARA_SD = standard deviation of PARA_MN; ENN_MN = Euclidean nearest neighbour mean distance; ENN_SD = standard deviation of ENN_MN. \cos^2 represents the contribution of a principal component to the squared distance of the metric to the origin. The closer the tip of an arrow of a metric to the circumference, higher is its contribution to one or more principal components. Metrics with arrows similar in direction and angle are more correlated, and metrics with arrows close to the PCA axes are those highly correlated to the axes.

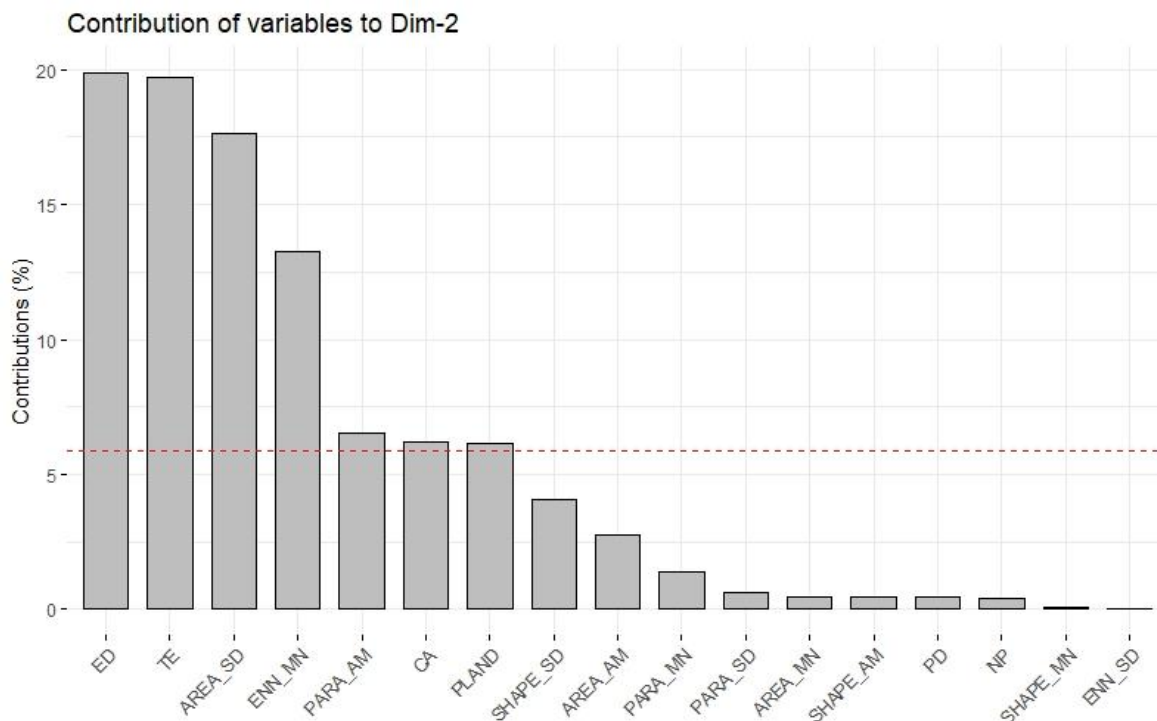
Appendix S5: Pair-wise correlation values between metrics of landscape structure and five most explanatory axes of the Principal Components Analysis. Metrics: CA = area amount (hectares); PLAND = percentage of forest cover respect to the total area of a landscape unit (1 km²); NP = number of patches; PD = density of patches; TE = total length of patch edges (m); DE = edge density; AREA_MN = area mean of the patch size; AREA_AM = mean-weighted area of the patch size; AREA_SD = standard deviation of AREA_AM; SHAPE_MN = index of mean form (SHAPE, calculates an index of complexity of the patch with respect to a standard); SHAPE_AM = index of mean-weighted form; PARA_MN = perimeter-area mean patch relationship; PARA_AM = perimeter-area mean-weighted patch relationship; PARA_SD = standard deviation of PARA_MN; ENN_MN = Euclidean nearest neighbour mean distance; ENN_SD = standard deviation of ENN_MN.

	Axis-1	Axis-2	Axis-3	Axis-4	Axis-5
CA	-0.85	0.44	0.17	0.21	-0.05
PLAND	-0.85	0.44	0.18	0.22	-0.05
NP	0.73	0.11	0.56	-0.15	-0.26
PD	0.73	0.12	0.57	-0.15	-0.25
TE	0.53	0.78	-0.23	-0.01	0.02
ED	0.53	0.79	-0.23	-0.01	0.02
AREA_MN	-0.91	0.12	0.11	0.34	-0.10
AREA_AM	-0.87	0.29	0.13	0.33	-0.01
AREA_SD	0.35	0.74	-0.01	-0.24	0.39
SHAPE_MN	0.49	-0.05	-0.82	0.22	-0.07
SHAPE_AM	0.67	0.12	-0.64	0.34	0.05
SHAPE_SD	0.78	0.36	0.37	0.26	0.11
PARA_MN	0.91	-0.21	0.13	0.21	-0.01

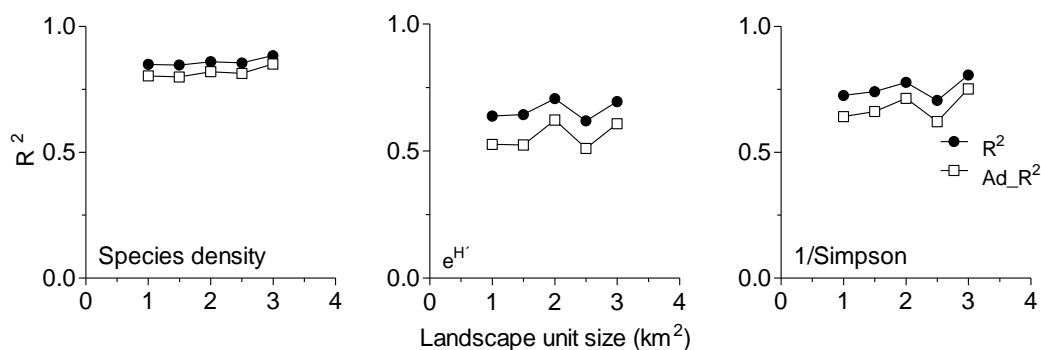
PARA_AM	0.80	-0.45	-0.12	0.17	-0.24
PARA_SD	0.73	0.14	0.47	0.12	0.22
ENN_MN	0.04	-0.64	0.23	0.17	0.61
ENN_SD	0.37	-0.01	0.24	0.86	-0.06



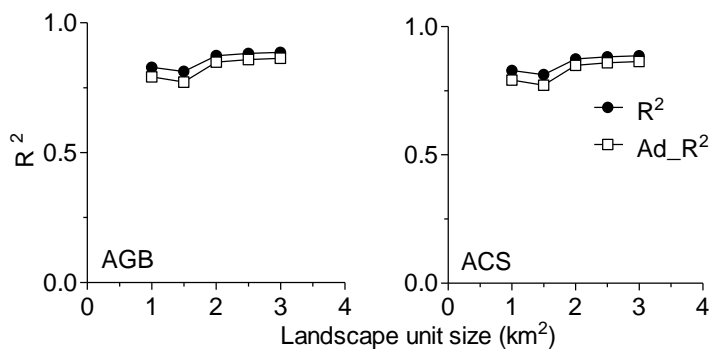
Appendix S6. Relative contribution (%) of landscape structure metrics to axis-1 of PCA. Metrics: CA = area amount (hectares); PLAND = percentage of forest cover respect to the total area of a landscape unit (1 km²); NP = number of patches; PD = density of patches; TE = total length of patch edges (m); DE = edge density; AREA_MN = area mean of the patch size; AREA_AM = mean-weighted area of the patch size; AREA_SD = standard deviation of AREA_AM; SHAPE_MN = index of mean form (SHAPE, calculates an index of complexity of the patch with respect to a standard); SHAPE_AM = index of mean-weighted form; PARA_MN = perimeter-area mean patch relationship; PARA_AM = perimeter-area mean-weighted patch relationship; PARA_SD = standard deviation of PARA_MN; ENN_MN = Euclidean nearest neighbour mean distance; ENN_SD = standard deviation of ENN_MN. The dotted red line represents the average contribution of all metrics (5.9%).



Appendix S7: Relative contribution (%) of landscape structure metrics to PCA axis-2. Metrics: CA = area amount (hectares); PLAND = percentage of forest cover respect to the total area of a landscape unit (1 km²); NP = number of patches; PD = density of patches; TE = total length of patch edges (m); DE = edge density; AREA_MN = area mean of the patch size; AREA_AM = mean-weighted area of the patch size; AREA_SD = standard deviation of AREA_AM; SHAPE_MN = index of mean form (SHAPE, calculates an index of complexity of the patch with respect to a standard); SHAPE_AM = index of mean-weighted form; PARA_MN = perimeter-area mean patch relationship; PARA_AM = perimeter-area mean-weighted patch relationship; PARA_SD = standard deviation of PARA_MN; ENN_MN = Euclidean nearest neighbour mean distance; ENN_SD = standard deviation of ENN_MN. The dotted red line represents the average contribution of all the variables (5.9%)



Appendix S8. Response of R^2 and adjusted R^2 of the model $Y = \text{PLAND} + \text{PLAND}^2 + \text{ED} + \text{ENN_MN}$ as a function of the spatial scale of LUs (1, 1.5, 2, 2.5 and 3 km²). Y = species density, left; number of common species ($e^{H'}$); effective number of dominant species ($1/\text{Simpson}$), right. For each size of LU, we associated the landscape metrics calculated at each corresponding size and the response at 1 km². We then, applied the model and obtained the R^2 and adjusted R^2 (Y-axis)



Appendix S9. Response of R^2 and adjusted R^2 of the model $Y = \text{PLAND} + \text{PLAND}^2 + \text{ED} + \text{ENN_MN}$ as a function of the spatial scale of LUs (1, 1.5, 2, 2.5 and 3 km²). Y = Aboveground Biomass (AGB), left; Aboveground Carbon Storage (ACS), right. For each size of LU, we associated the landscape metrics

calculated at each corresponding size and the response at 1 km². We then, applied the model and obtained the R² and adjusted R² (Y-axis)

Appendix S10: Effects of changes in landscape composition (percentage of forest cover -PLAND- and PLAND²) and configuration (edge density in forest patches -ED- and inter forest patch connectivity -ENN_MN-) metrics on tree species diversity (q₀ = species density, q₁ = number of common species, and q₃ = number of dominant species), aboveground biomass (AGB), and aboveground carbon storage (ACS) over the forest-to-agriculture conversion, considering landscape units of 1, 1.5, 2, 2.5 and 3 Km². In all cases, LMs were fitted, using landscape metrics as independent regressors. The significance of the parameters and the proportion of the variation explained of each independent variable and the whole model (R²) are shown. ***: p< 0.001, **: p<0.01 and *: p<0.05. Only significant parameters are shown.

1 km ²	Var	q ₀	R ²	q ₁	R ²	q ₂	R ²	AGB	R ²	ACS	R ²
	Intercept	-17.2		5.7		1.6		-166635.3		-78985.1	
	PLAND	1.49 ***	0.71	0.54***	0.41	0.04**	0.38				
	PLAND ²	-0.005**	0.11	-0.00**	0.29	-0.00*	0.22	114.5***	0.80	54.3***	0.80
	Model		0.82		0.70		0.60		0.80		0.80
	Residuals		0.18		0.30		0.40		0.20		0.20
1.5 km ²											
	Intercept	-27.8		4.41		2.18		-222997.69		-105700.90	
	PLAND	2.10***	0.72	0.60***	0.43	0.05**	0.40				
	PLAND ²	-0.0104**	0.11	-0.00**	0.29	-0.00*	0.24	132.58***	0.80	62.84***	0.80
	Model		0.83		0.72		0.64		0.80		0.80
	Residuals		0.17		0.28		0.46		0.20		0.20
2 km ²											

Intercept	-11.26		-9.33		1.24		145880.62		69147.41	
PLAND	1.94***	0.78	0.25***	0.49	0.03***	0.43				
PLAND ²	-0.01*	0.07	-0.00**	0.19	-0.00*	0.18	125.17***	0.87	59.33***	0.87
ENN_MN			0.09*	0.08						
Model		0.85		0.70		0.61		0.87		0.87
Residuals		0.15		0.30		0.39		0.13		0.13

2.5 km²

Intercept	-14.91118891		-2.86623		1.47		134100.63		63563.7	
PLAND	1.75***	0.79	0.27***	0.50	0.03**	0.44				
PLAND ²	-0.006*	0.05	-0.00*	0.17	-0.00*	0.15	131.29***	0.87	62.23***	0.87
Model		0.84		0.67		0.69		0.87		0.87
Residuals		0.16		0.33		0.31		0.13		0.13

3 km²

Intercept	-41.3		-19.86		0.56		117792.18		55833.49	
PLAND	1.46 ***	0.81	-0.1***	0.51	0.02***	0.45				
PLAND ²	-0.003*	0.04	0.00**	0.16	0.00*	0.14	137.1***	0.87	64.98***	0.87
ENN_MN	0.33	0.03	0.15*							
Model		0.88		0.67		0.59		0.87		0.87

Residuals

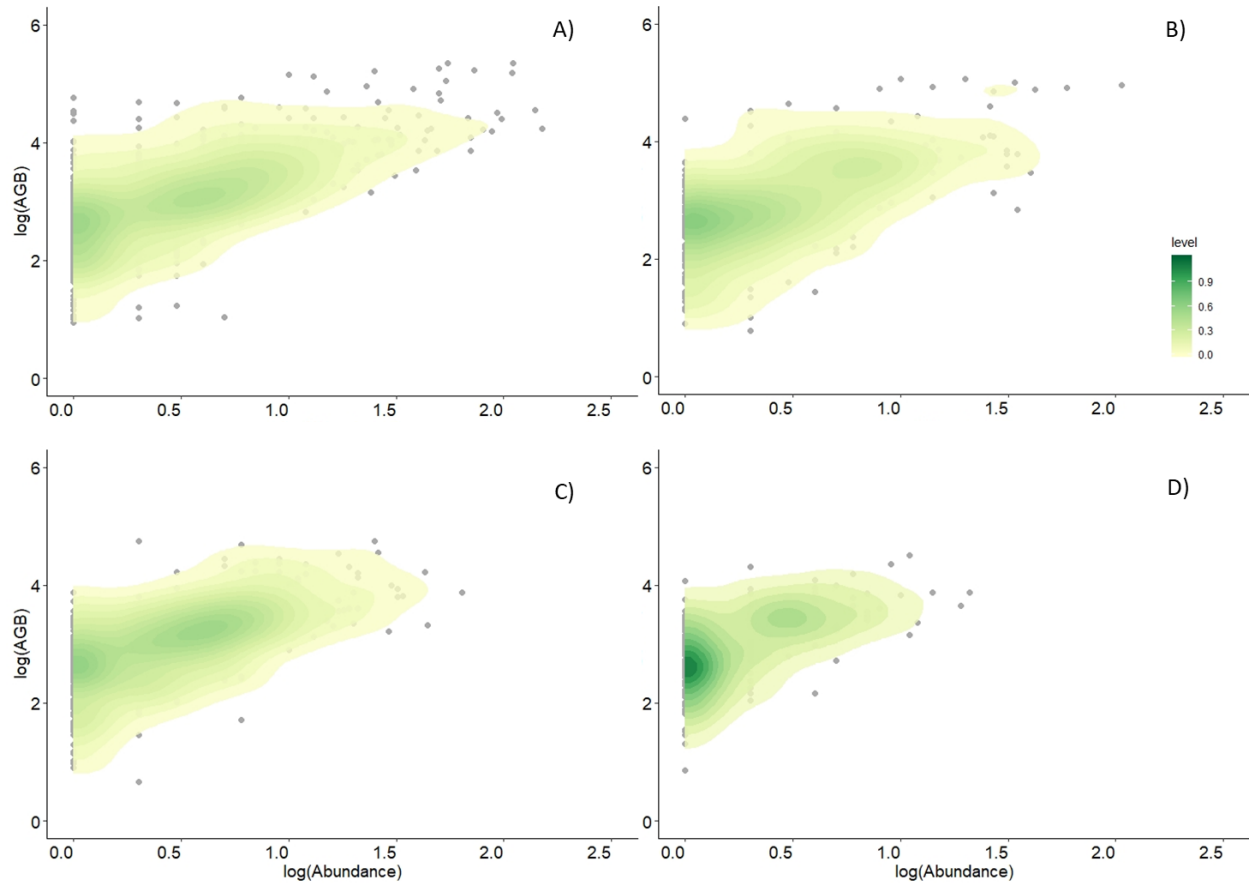
0.12

0.33

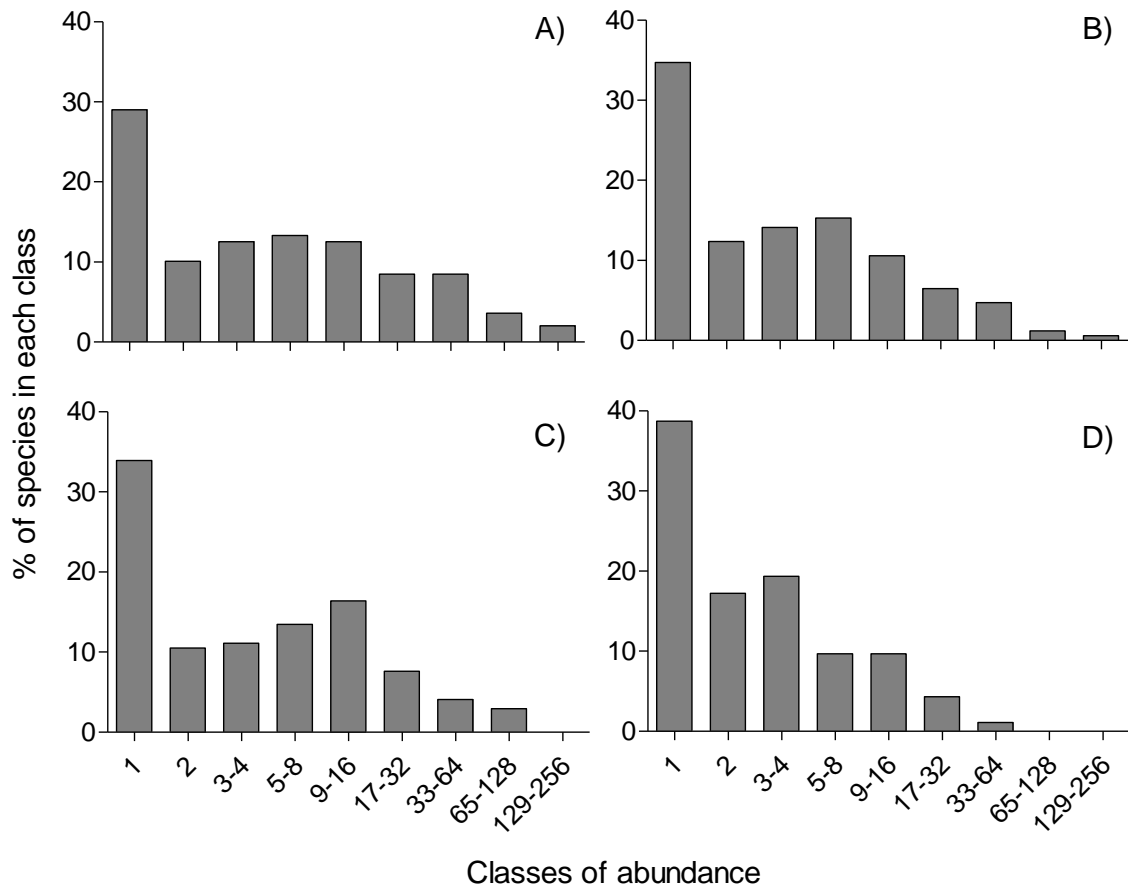
0.39

0.13

0.13



Appendix S11: Density-shaded scatter plots of the absolute AGB of tree species (Mg/2.12 ha) as function of their absolute population density (trees/2.12 ha) for LUs with: A) 75-100%, B) 50-75%, C) 25-50%, and D) 0-25% forest cover. Note the Y and X axes are in \log_{10} scale. Dots represent individual species. Darker colour areas represent increasing levels of crowding dots.



Appendix S12: Relative frequency of species by classes of population density in LUs grouped by categories of percentage of forest cover in the landscape: A) 75-100%, B) 50-75%, C) 25-50% and D) 0-25%. Note: X-axis is in geometric scale.

Capítulo 3: ¿Qué impulsa las decisiones de manejo y la variabilidad del rendimiento de grano en los sistemas de cultivo de maíz tropical? Evidencia de agricultores a pequeña escala en el sur de México

Artículo enviado a “Agricultural systems” como:

Wies, Germán^{1*}; Ceccon, Eliane²; Navarrete-Segueda, Armando¹; Larsen, John¹, Martinez-Ramos, Miguel¹ (2021). What drives management decisions and grain yield variability in Neotropical maize cropping systems? Evidence from small-scale farmers in Southern Mexico.

What drives management decisions and grain yield variability in Neotropical maize cropping systems? Evidence from small-scale farmers in Southern Mexico

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Abstract

Small-scale cropping systems show enormous challenges for obtaining efficient, stable, and predictable responses in grain yields due to their great biophysical, management and socioeconomic complexity. In the Neotropics, traditional managements have incorporated modern agricultural practices; however, the efficacy of these tools on grain yield and systems' sustainability is unknown. In this sense, we explored biophysical, agronomic and socioeconomic drivers determining the maize cropping system and grain yield in Southern, Mexico. The specific objectives were i) to investigate the effects of geopedologic soil characteristics on maize grain yield, ii) characterize tropical maize cropping systems and model how agronomic factors determine grain yield variability, and iii) explore if underlying socioeconomic drivers determine the agronomic ones and, in consequence, the maize cropping systems. On-field interviews and soil data from geopedologic unit maps were used, from maize cropping systems in Chiapas, Mexico. Structural equation modelling (SEM), quantitative and qualitative analyses were used to explore the whole data set. We found that cropping systems differentiated as conventional (CS) and traditional (TS). Soils determined grain yield variability independently the cropping systems. Most common agronomic inputs expected to positively impact on grain yield were not effective in any cropping system. In CS, neither pesticides nor fertilization determined the crop grain yield. Plant density explained 72% of crop grain yield variation. In TS, grain yield related negatively with plant density (-0.59) while the fallow period slightly explained grain yield. We identified that cultural practices acquired by the farmers in their birthplace determine the type of the current maize cropping system. We highlight inconsistent modern agronomic management of tropical maize cropping systems where agrochemical inputs (fertilizers and pesticides) do not

translate in higher grain yield nor systems' sustainability. New theoretical models for small-scale maize cropping systems incorporating socioeconomic and cultural drivers might be necessary to predict better maize grain yield.

Keywords: traditional cropping systems; structural equation models, socioeconomic drivers; agronomic drivers, biophysical drivers, Chiapas

1. Introduction:

Maize (*Zea mays L.*) crops occupy the first places in cultivated area in the most populated tropical countries in the world (India, Indonesia, Brazil, Nigeria, Mexico, Ethiopia, Philippines, Vietnam, Thailand and Tanzania, "FAO stats," 2021). In these countries, maize cropping systems vary from indigenous or traditional to those highly technified, and from small scales (<2 ha) to large extensions (Ricciardi et al., 2018b, 2018a). In small-scale systems, it is still difficult to develop accurate agronomic predictive models, since biophysical factors including soil properties, water availability, temperature and radiation, interact with a wide variety of agronomic and cultural managements, affecting maize grain yield. For example, in western Kenya, in low-inputs maize cropping systems, low soil N and P was the main constraint in grain yield (P. Tittonell et al., 2008; Pablo Tittonell & Giller, 2013). However, fertilization experiments in this region showed that interactions between soil fertility, usual fertilization rates

and the amount of precipitation triggered a high variability of grain yields. These results suggest that site-specific agronomic recommendations are needed to avoid low nutrient use efficiencies, low yields and food insecurity (Njoroge et al., 2017).

Agronomic management decisions (genotype, sowing date and plant density and the strategy and timing of agrochemical applications) also strongly affect grain yield. Affholder et al. (2013) showed that maize grain yields in family systems in the tropics may be constrained due to agronomic (weed infestation and poor soil fertility) more than biophysical factors (radiation, rainfall or temperature). Genotype election often appears as a conflicting management issue. On one hand, classical agronomy research and extension agencies aim to improve and recommend high-yielding maize hybrids but small-scale farmers often choose low-yielding local landraces (Abakemal et al., 2013; Ndoli et al., 2019). This is because these varieties have other preferred traits such as low inputs requirements, pest resistance, cycle duration, longer storage durability and better grain taste and flavour (Abakemal et al., 2013; Bellon & Hellin, 2011; Eakin et al., 2014; Mulatu & Zelleke, 2002). On the other hand, when small-scale farmers choose maize hybrids, often, they sow lower plant densities than those defined as optimum constraining reachable grain yields (Seyoum et al., 2019). Finally, the crop protection strategy through pesticides is also a conflictive issue between agronomic recommendations and farmer decisions. In Central Malawi, herbicides has been promoted for weed control, labour saving and even reduce land degradation, however, in farms where were most applied, casual labours were not needed creating unemployment and food insecurity (Bouwman et al., 2020).

In southern Mexico, an important area of the maize hotspot and maize origin centre, coexist two main maize cropping systems (Bellon & Hellin, 2011). The “conventional cropping systems” (CS), small-medium scale systems mainly determined by the use of commercial hybrids and mechanical labour and the “traditional cropping systems” (TS), small-scale systems mainly determined by the use of landraces (“Tuxpeño” landrace is commonly used in these systems, <https://conabio.shinyapps.io/conabio-pgmaices1/>) and manual labours (Brush & Perales, 2007). Several agronomic strategies (some promoted from government and some from companies to foster production) have been applied to both tropical maize-cropping systems. Relevant factors such as livelihoods, socioeconomic and also genetic have been studied in these cropping systems (Birol et al., 2008; Dutta et al., 2020; Eakin et al., 2015; Falkowski et al., 2019; K. Mercer et al., 2008; K. L. Mercer & Perales, 2010). However, the evaluation of the agronomic drivers that interact with each other in order to detect their effectiveness on grain yield is still unknown. Structural equation models (SEM) allow evaluating this framework since the intervening variables can function as explanatory and response variables simultaneously. Furthermore, the partial and indirect effects of these variables can be quantified. Agronomic management decisions and inputs may have a rational basis subjected to obtain grain yield. However, they may be determined by multiple underlying socioeconomic and cultural factors that finally affect the habits, preferences and farmers decisions (Banerjee et al., 2014; Bellon & Hellin, 2011; Brush & Perales, 2007; Dutta et al., 2020; González-Esquivel et al., 2015). As described, there is a big body of knowledge generated studying biophysical, agronomic and socioeconomic drivers in small-scale maize cropping systems in tropical regions of Africa (e.g. Malawi, Kenia, and Nigeria). However, there is a gap about how biophysical drivers interacting

with agronomic factors affect the grain yield variability of maize cropping systems in the humid tropical regions of America (Neotropics). The Neotropic is the centre of origin and domestication of maize. In this region, pre-Hispanic maize systems have currently incorporated modern agronomic management strategies derived from the green revolution. Thus, we consider it of paramount importance to analyse how maize cropping systems present in an extensive region of the Neotropic respond to the biophysical environment and agronomic management strategies. Furthermore, the inclusion of socioeconomic and cultural factors could provide a comprehensive understanding of the current state of these systems.

Thus, the objectives of this study were to i) investigate the relative importance of soil characteristics on grain yield, ii) characterize tropical maize cropping systems modelling their agronomic factors determining grain yield variability, and iii) to identify underlying socioeconomic or cultural drivers, which determine the agronomic drivers and in consequence the maize cropping system. In the Figure 1 is shown a conceptual framework of the expected direct or indirect effects of biophysical, agronomic and socioeconomic drivers in tropical maize cropping systems. We expect that changes in soil resources will have direct effects on grain yield but also indirect effect through agronomic management responses (e.g. fertilization, hypothesis 1). In the same way, agronomic inputs and management decisions will have direct effects on grain yield (hypothesis 2). Finally, we expect that socioeconomic and cultural factors will have an indirect effect, through its influence on farmer decisions for using agronomic inputs and for crop management (hypothesis 3).

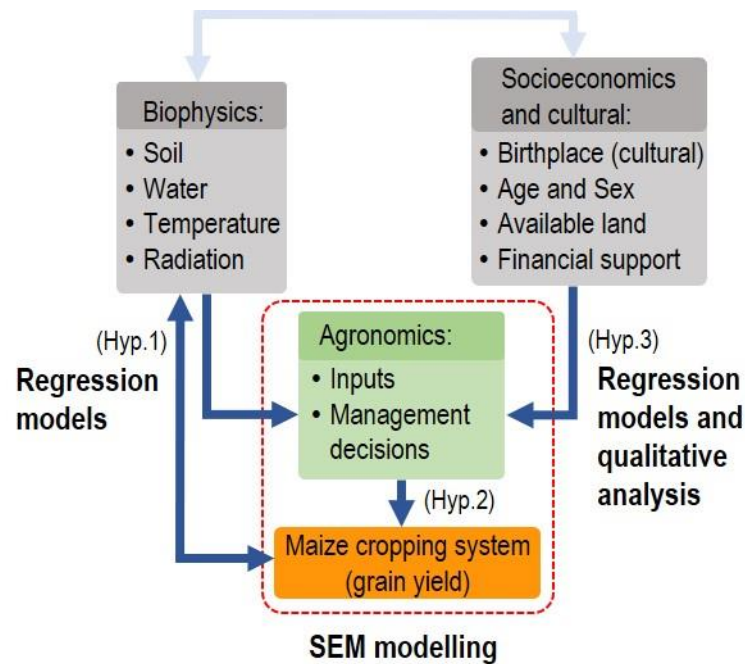


Figure 1: Conceptual framework used to integrate biophysical, agronomics and socioeconomic drivers affecting (blue arrows) the type and the performance of the maize cropping systems. Light blue arrow indicates presumably relationships that indirectly could affect the maize cropping systems (not evaluated). Dashed red line box indicates where SEM were applied. See material and method specifications for SEM applied to CS and TS.

2. Materials and methods:

2.1 Study area:

The Neotropical, Marqués de Comillas region (MDC) (16°54'N, 92°05'W), southern México covers an area of ~2,008 Km² (Fig 2). Mean annual precipitation is ca. 3000 mm and mean monthly temperature is 22°C (Martínez-Ramos et al., 2009). Since 1970 onwards, MDC was part

of a government land distribution program and experienced a migration process of people from different states of Mexico (Chiapas, Guerrero, Jalisco, Michoacán, Oaxaca, Tabasco) and Guatemala (de Vos & Marion, 2015). After 1970, MDC experienced a fast deforestation-to-agriculture process reducing tropical rainforest to less than 35% by 2013 (Julia Carabias et al., 2015). Currently, ~70% of the region is covered by agricultural land uses, forest patches, and human settlements (Zermeño-Hernández et al., 2016).

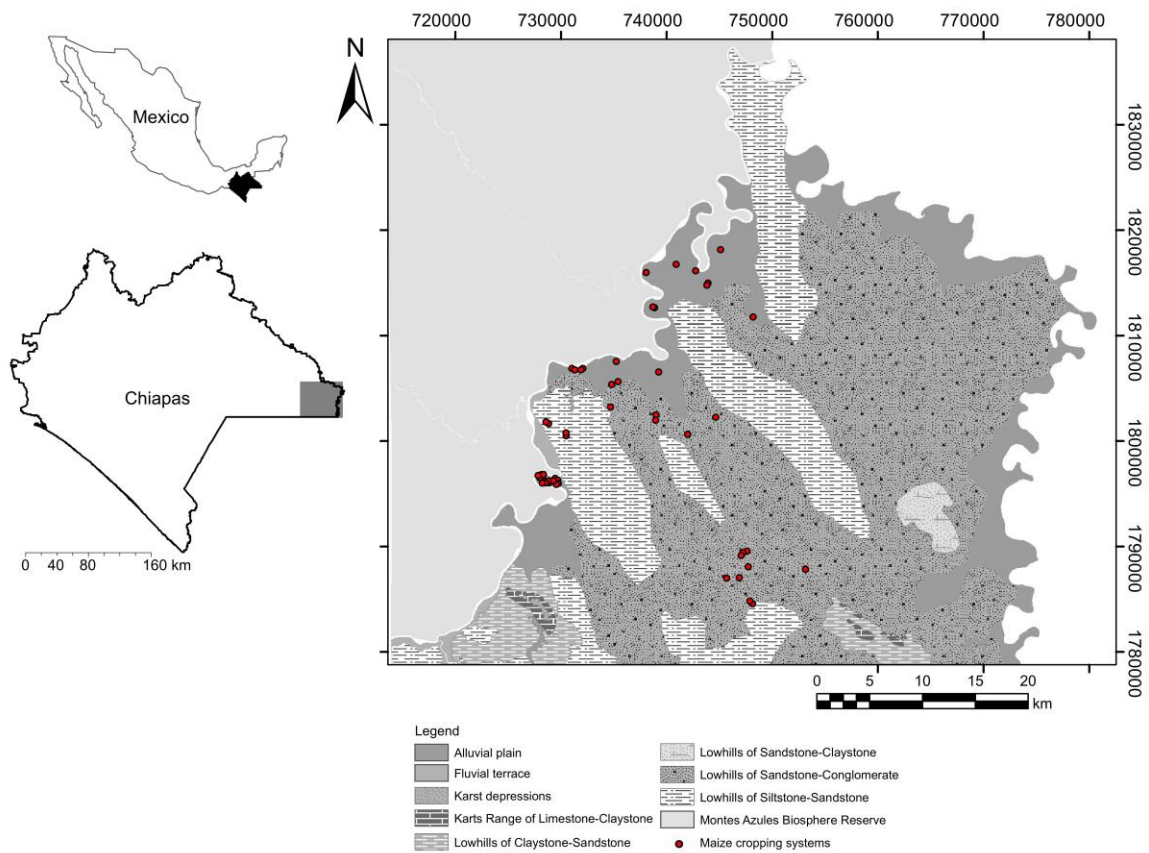


Figure 2: Neotropical region of Marqués de Comillas in the Southern Mexico. Geopedologic units and maize cropping systems (red points) are specified.

2.2 Maize cropping system characterization

Fifty-one interviews were performed in the MDC in five *ejidos* (communities). At least nine interviews were performed by *ejido*. To characterize the maize cropping systems, we designed a semi-structured interview aiming to describe the whole incurred variables (Manzini, 2003). We asked for the soil labour management (manual, mechanical), maize genotype, plant density and grain yield. Moreover, we asked for types, amount, and application frequency of supply inputs (fertilizers, herbicides and insecticides). In cases when necessary, we asked about the amount labour applied in terms of journals (1 journal = 8 hours of labour) or the diesel liters incurred in mechanical labour such as plowing, seeding and harvesting. We also registered other management practices such the fallow period, fire times and rotations sequences.

For grain yield we wanted to record with the highest possible accuracy, hence, we asked about the highest and the lowest grain yield obtained with those practices. These values served to check if farmers had a reasonable understanding of the magnitudes they were obtaining. For supply inputs, it was easier because farmers use recommended quantities of, for example, bags of UREA. Additionally, we asked about total farm area, birthplace (taking into account that most of the farmers born and lived -at least a reasonable time- out of MDC), the year of migration and the frequent practices and uses in their previous locality.

When we carried out the interviews, we toured the countryside together with the farmer at the time we were asking the questions. This tour served to visually check the information they were answering (e.g. type of insecticide and amount) and to georeference the vertices of the farm to then, check the crop extents. As farmers answered in different units or quantities they were

familiarized (e.g. number of bottles of used insecticides), when necessary, quantitative recorded variables were recalculated in common units (e.g. from bags of fertilizer to kg N ha^{-1}). Similarly, for agrochemicals, we registered the brand and then calculated the amount of active principle applied.

To ensure that the sample size was representative of Neotropic-Mexican maize cropping systems, we performed variance accumulation curves as a function of the increasing number of interviews (Fig S1). All the variables that would hypothetically affect maize grain yield were tested (see below agronomic driver's models and predictions). From 20 to 30 interviews, the variance and the mobile means of grain yield, plant density, applied nitrogen and phosphorus, herbicides, insecticides, manual weeding, frequency of fires and fallow time were stabilized. Therefore, 51 interviews were an adequate sample size of the Neotropic-Mexican maize cropping systems (Fig S2).

2.3 Soil characterization

To characterize soils of maize cropping systems, we based on a map of geopedologic units published by Navarrete-Segueda et al., (2018). We enlarged this map delineating the geopedologic units by visual interpretation of the external characteristics of the landscape (Zinck et al., 2015). We also used aerial photographs (1:20000) and a 1:50000 digital elevation model. Matching the georeferenced vertices of farms with the map, we assigned one geopedologic unit to each maize cropping system (see Fig 2). Geopedologic unit samplings, laboratory procedures and soil chemical analysis are detailed in APENDIX.

2.4 Data analysis

Maize cropping systems characteristics. To explore potential different maize cropping systems, we carried out a principal component analysis (PCA) with all recorded quantitative variables present in the pool of interviews (Abdi & Williams, 2010). Some farmers did not answer all questions (variables), because they did not know the requested information, or they never had recorded it. We estimated the missing values with missMDA R package. This algorithm allows to estimate missing values based on the data structure (not in averages) through an iteration procedure (Josse & Husson, 2012).

Identifying agronomic drivers, models' definition and predictions. With PCA we were able to identify bundles of variables associated to the cropping systems observed at field. We tested hypothesis 2 in CS and TS separately. We conceptualized models with agronomic coherence. For CS, manual weeding and total herbicides are expected to be reduced with higher plant densities (“crop protection light blue boxes”, Fig 3A) (Johnson et al., 1998; Sikkema et al., 2008). Grain yield is expected to positively correlate with manual weeding, total herbicides and insecticides. For the resources limiting potential yield (green boxes) both, plant density and total fertilizers are expected to positively impact on grain yield (Fig 3A). In TS, for the crop protection boxes, we expected a positive relationship between grain yield and total amount of herbicides and insecticides. For the resources limiting potential yield (green boxes), we expect for all, plant density, fallow period and total amount of fertilizer positive effects on grain yield (Fig. 3B). In addition, fire times is expected to negatively affect the grain yield. This variable involves crop

protection in the weed control in the pre-seeding period (light blue boxes) but also limits the potential of grain yield by decreasing the brushwood produced in the fallow (green boxes, Fig. 3B). These proposed conceptual models incurred multiple quantitative variables, which were functioning as explanatory, but also as responses. Therefore, Structural Equation Models are an appropriate approach to assess our predictions (Shipley, 2016).

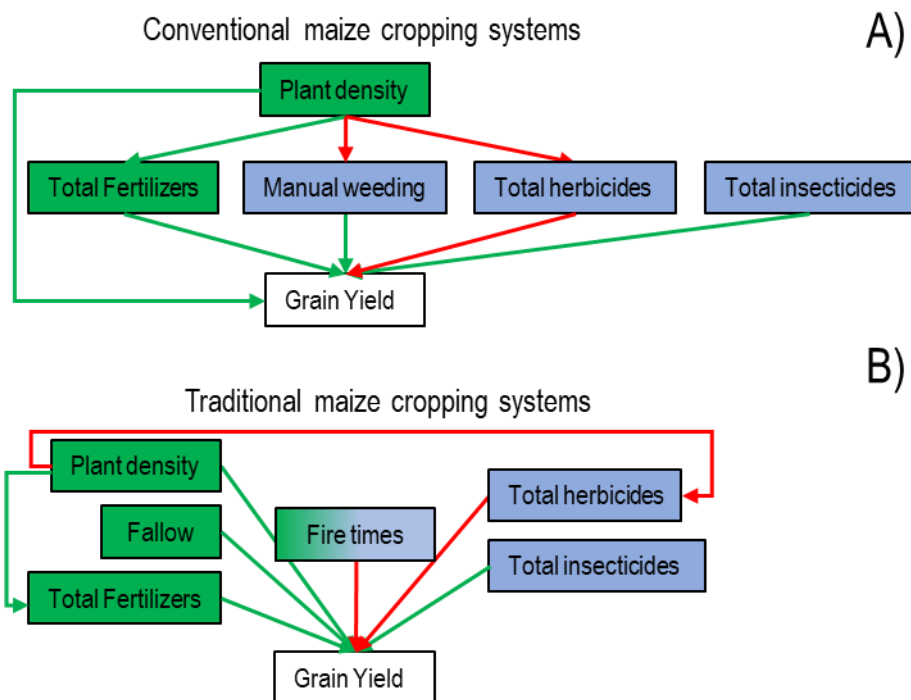


Figure 3. A) Expected models for CS and TS to test hypothesis 2. Green arrows indicate positive relationships and reds, negative. Blue boxes indicate crop protection variables, green boxes indicate resources limiting potential yield. The fire times has both colours because it limits the soil fertility but also is used as weed management.

Describing socioeconomic drivers associated to agronomic ones. We explored relationships between socioeconomic drivers (farmers' birthplace, age and gender, the total available land for different activities and type subsidy program) and agronomics (mechanical labour in liters of

diesel, manual labour, total journals, total fertilizer, herbicides and insecticides, fallow period and maize type). We combined all socioeconomic drivers as explanatory and agronomic as response variables. We used ANOVA in those cases when socioeconomic was a categorical variable and linear regressions when both variables were quantitative. The relationships between gender and agronomic responses were not included because only four women were present in the sample creating unbalanced data. This fact agrees with the low women's land tenure proportions (19%) present in Mexico (Hamilton, 2002).

Describing farmers' birthplace associated to maize cropping systems. Once main drivers were detected from the PCA, the coordinate plot of the PCA showed that some variables were lumped by *ejidos* (Fig 5B). We constructed a decision tree classification based on main variables present in the *ejidos* that we suspected were associated to their birthplaces (see Supp Fig 6). For example, many farmers in San Jose *ejido* combined maize crops with secondary forest or most of farmers in Reforma Agraria used machinery for the soil labour. With this approach, each cropping system was classified by “Traditional”, “Conventional”, “Mixed” and “Shifting agriculture”. To explore possible relationship between the birthplace and the current cropping system, we performed an alluvial diagram (Brunson, 2020). We used the cropping system classification, the current *ejido* where the farmer worked and the information of State and Municipality of birth.

3. Results

3.1 Direct effects of geopedologic units and indirect effects of fertilization on maize grain yield variability (Hyp. 1)

Maize cropping systems were distributed along two main geopedologic units. The geopedologic unit described as Alluvial plains have soils next to rivers that with some frequency, receive sediments from flooding in the wet seasons. This temporal dynamic explains their highest levels of C, N and the neutral-alkaline pH (Table 1). Conversely, the geopedologic unit described as Low hills of sandstones have lower values of these characteristics, due their elevated percentages of sand and Al saturation. These later may explain their lowest pH and CEC (Sierra et al., 2003).

Table 1: Soil properties (mean and standard error, SE) for two geopedologic units in MDC, southern, Mexico. C, percentage of soil carbon; N, percentage of total nitrogen; P, extractable total phosphorus (Bray-Kurtz); pH, pH in soil suspension; CEC, Cation exchange capacity; Sand, percentage of total sands (> 2 mm); Al, percentage of aluminium saturation.

Variable	Alluvial plain		Low hills of Sandstone	
	Mean	SE	Mean	SE
C (%)	2.88	0.07	1.01	0.02
N (%)	0.22	0.01	0.13	0.00
P (mg kg ⁻¹)	1.41	0.15	1.76	0.13
pH (H ₂ O)	7.12	0.13	5.13	0.18
CEC (cmol kg ⁻¹)	109.96	25.99	18.50	7.22
Sand (%)	32.16	24.41	57.23	10.25
Al (%)	0.65	0.65	10.98	0.01

Aiming to correct these soil deficiencies farmers apply significantly more fertilizers in the low hills than in the alluvial plains (Fig 4A). When we related grain yield as a function of the amount of applied fertilizers grouping by geopedologic units, significantly different intercepts indicated that yields were greater in the alluvial plains compared to the low hills ($p < 0.0001$, Fig 4B). However, grain yield responded similarly to the increasing fertilizer supply in the different geopedologic units since the slopes did not differ between them (general slope, $p = 0.157$, Fig 4B).

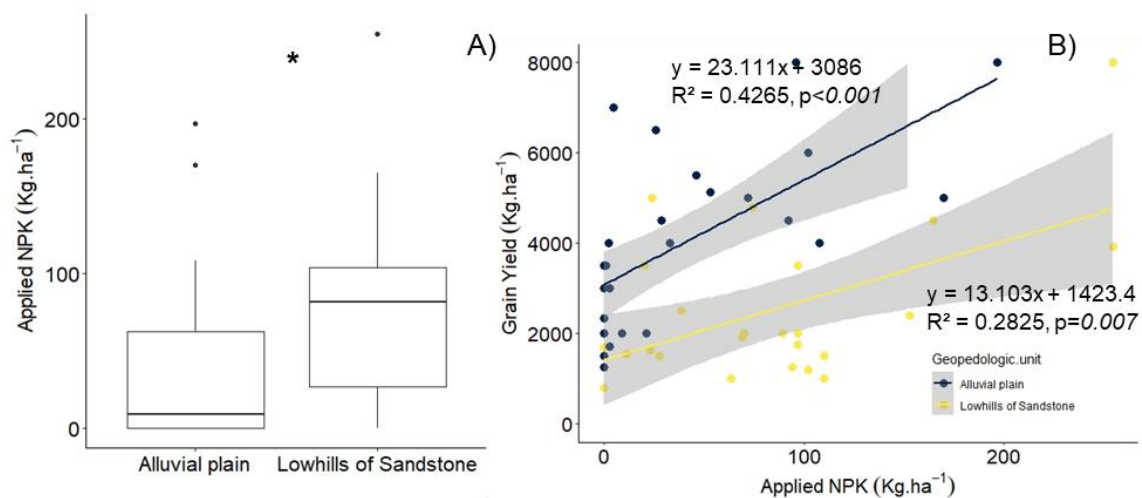


Figure 4. A) Box-plot of total applied fertilizers (NPK, kg ha⁻¹) in maize fields in alluvial and low hill geopedologic units (*, $p < 0.05$). B) Maize grain yield (kg ha⁻¹) as a function of the total applied fertilizers (NPK, kg ha⁻¹) in maize cropping systems gathered by geopedologic units. Blue dots, alluvial soils and yellow, low hills of sandstone. Grey area represents the 95% of confidence intervals. p values and the R^2 are detailed.

3.2 Describing Neotropical maize cropping systems

From the PCA analysis, the correlation variables plot and observations plot are shown in figure 5 A and B. In the left-bottom side of the variable correlation plot, there were grouped variables associated with manual labour, such as journals of manual harvest, plowing, seeding and weeding (Fig 5A). In the same direction but in the top, there were ordered the use of maize landraces (genotype), total maize cycles in one year (two cycle for landraces), the fallow period and the fire times. Thus, in the left side there was characterized the TS. To the right side, mechanical labour variables, i.e. diesel litres for seeding, ploughing and harvesting were positively correlated to component-1. On the same side, increasing maize area (maiz_ha), plant density (dens_pl_ha) and higher grain yields (yield) were grouped, defining CS. Total amount of herbicides and insecticides, and their associated management variables (number of applications and incurred journals) were closer to the component-2 and not associated to any cropping system since they did not differ in the applied amount (Supp Fig 2A and B). Total amount of fertilizers (NPK) did correlate with neither component-1 nor 2.

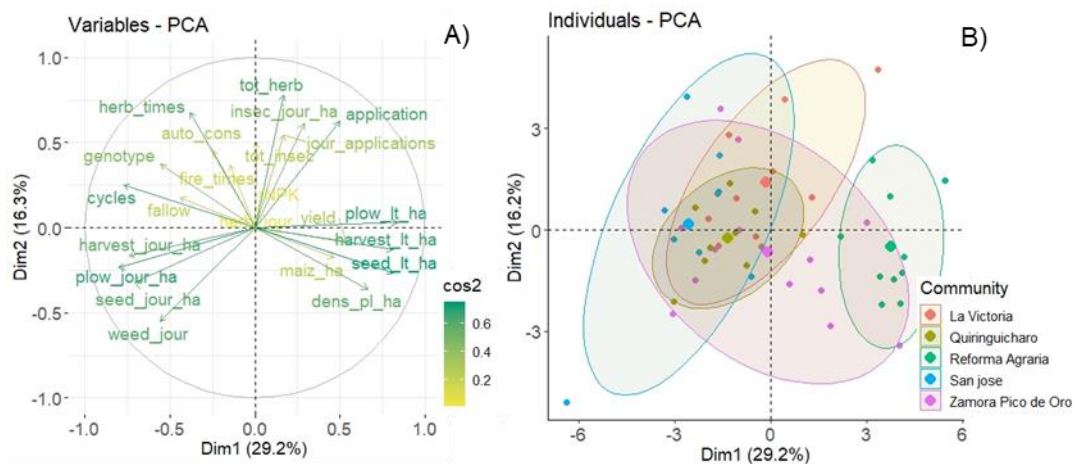
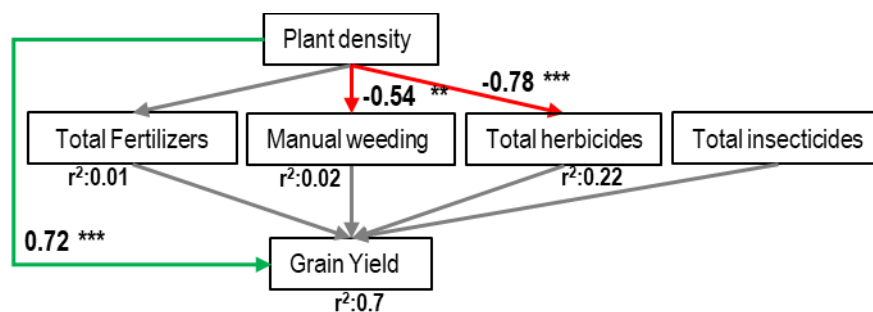


Figure 5: A) Correlation plot of agronomic variables resulted from the PCA (Abdi & Williams, 2010). \cos^2 represents the quality of representation of each variable to the principal component-

1. The more yellow variables are not well represented by component-1, the greener variables are better represented. The closer the angle between arrows the more correlated they are. B) Coordinates plot from the agronomic variables PCA. Each dot corresponds to one maize cropping system. Ellipses distinguish the farming systems between *ejidos* (communities). Conventional cropping systems determined in the axis-1 to the right are mainly present in *ejido* “Reforma agraria” (green points) and some of Zamora Pico de Oro (violets points). Traditional maize cropping systems determined to the left in the axis-1 are mainly in *ejidos* San Jose (light blue points) and Quiringuicharo (light brown points)

3.3 Modelling agronomic drivers determining maize grain yield variability (hyp.2)

CS and TS were classified regarding the maize genotype use (landraces or hybrids). We tested hypothesis two in CS by using SEM. *p-value* of the model was ~ 0 hence, maize cropping systems data did not support the proposed model although some individual relationships did so (Fig 6). When increasing plant density both, manual weeding and total applied herbicides were significantly reduced. However, these crop protection management drivers neither total applied insecticides significantly affected the grain yield (grey arrows, Fig 6). Also, grain yield was not affected by total fertilizers (Fig 6). The main driver in CS was the plant density explaining 72% of variation in grain yield.



Fisher's C = 97.889 with P-value ~ 0 and on 24 degrees of freedom

Figure 6: Piecewise structural equation model applied to the proposed model for conventional maize cropping systems. Standardized coefficients with significance level ($*p < .05$; $**p < .01$; $***p < .001$) are given for green, positive, and red, negative relationships. C-Fisher coefficient and p -value significance of the model are provided.

We evaluated TS by applying SEM as well. Observations did not support the whole proposed model ($p \sim 0$, Fig 7). Total herbicides and fire times affected negative and significantly the grain yield. Neither total insecticides nor total fertilizers affected the grain yield. The fallow period was slightly significant and finally, as contrary expected, by increasing plant density, the grain yield was negatively affected (Fig 7).

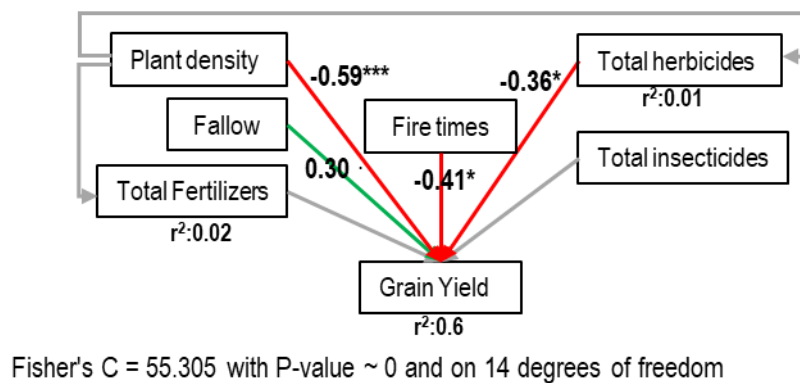


Figure 7: Piecewise structural equation model applied to the proposed model for traditional maize cropping systems. Standardized coefficients with significance level ($*p < .05$; $**p < .01$; $***p < .001$) are given for green, positive, and red, negative relationships. C-Fisher coefficient and p -value significance of the model are provided.

3.4 Relationships between socioeconomic and agronomic drivers

To evaluate hypothesis 3, we explored all possible relation between socioeconomic and agronomic drivers. Farmers who were born in the *ejidos* (youngers) used more diesel incurred in mechanical labour than farmers born abroad (one exception were farmers from Oaxaca, Fig S5A). Farmers with “PROGAN” subsidy applied more herbicides than farmers with or without other subsidy (Fig S 5B).

3.5 Describing the farmer’s birthplace with their maize cropping systems

To find out if communities had a predominantly cropping system, the observation in the PCA were grouped by *ejidos* and plotted in a coordinate graph (Fig 5B). Reforma Agraria cropping systems were positioned to the right side of the graph and close to the component-1 indicating that variables of the CS were mostly driven by this *ejido* (Fig 5A and B). Zamora Pico de Oro samples had a wide variation of cropping systems (from conventional to traditional) ranging from the left to the right of the component-1. Quiringuicharo and San Jose set their cropping systems in the left of the plot carrying weight to the TS. At both *ejidos* many (predominantly in San Jose) farmers allow the fallow for more than twelve months indicating the shifting agriculture practice (Fig 5B).

We then, classified maize cropping systems in terms of three main used management practices: the maize genotype (landraces or commercial hybrids), the fallow period (less or more than twelve months) and the use of mechanical or manual soil labour. All cropping systems were classified by these conditionings following a tree decision as specified in Fig S6. Numbers of

farmers with CS and TS systems were 15 and 16, respectively. In addition, farmers with shifting agriculture and with mixed features of CS and TS systems were 12 and 8, respectively.

To explore birthplace and maize cropping systems we plotted an alluvial graph (Fig 8). Reforma Agraria and San Jose *ejidos* had predominantly CS and Shifting agriculture cropping systems, respectively. For these *ejidos*, most farmers had the same birthplace (Fig 8). Zamora Pico de Oro, which had a wide variation along the component-1 (Fig. 5B) showed all maize cropping systems types but also farmers arrived from four of the six states present in the interviews (Fig 8). Finally, La Victoria and Quiringuicharo presented mostly TS and mixed cropping systems, although the origin of the farmers was quite diverse for both *ejidos* (Fig. 8).

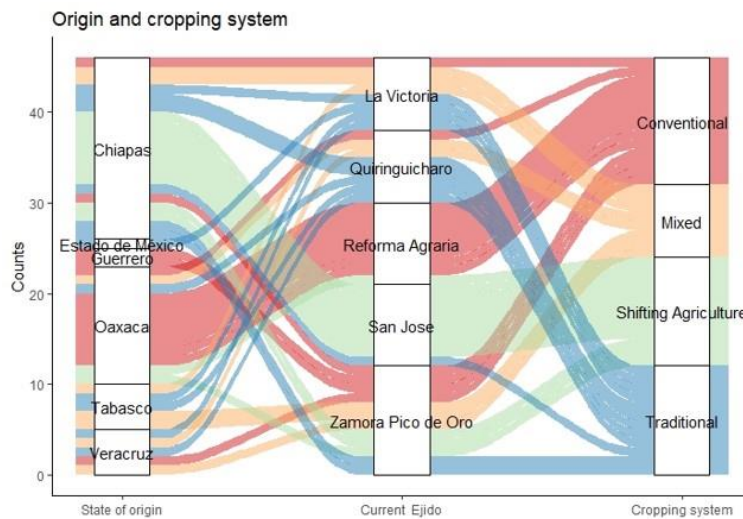


Figure 8: Alluvial diagram describing the farmer origin and the counts of cropping systems in each *ejido*. From left to right, the state of origin, the current *ejido* and the used cropping system for each interviewed farmer is shown. Colours indicate each cropping system (red, Conventional; yellow, Mixed; green, Shifting agriculture and blue, Traditional).

4. Discussion

We studied how biophysical, agronomic and socioeconomic drivers affect the maize cropping systems in a Neotropical region of Mexico. We found that soil quality is a strong factor determining maize grain yield; however, fertilization corrections are very diverse without any predictable response on grain yield. Maize grain yield was not responsive to herbicides nor pesticides in any cropping systems and plant density was the main driver affecting positively in CS and negatively in TS, the maize grain yield. In addition, the birthplace was a peculiar driver determining the type of maize cropping system. Below, we discuss the results in relation to the proposed framework and compare them with the small-scale maize cropping systems mainly developed in the African tropics (the most studied region of small-scale tropical maize cropping systems).

Soil properties and maize grain yield

Since neither precipitations in the wet seasons nor the length-day are not restrictive for yields determination in the tropics, geopedologic units arose as the main biophysical driver to affect the maize grain yield. In MDC region geopedologic units were the main driver determining natural primary productivity (Navarrete-Segueda et al., 2018). The alluvial plains and the low hills showed contrasting soil properties (Table 1). However, tropical maize cropping systems (sometimes mixed with other species) are frequently grown in these soils in the Neotropics (Kass & Somarriba, 1999). In average, grain yield in alluvial plains was 1.8 times greater than in low hills, independent of the maize cropping systems. Both geopedologic units showed low P levels for maize crops (Kaizzi et al., 2012). These low P levels are similar to those found in Kenya by

Tittonell et al., (2008) and Tittonell and Giller in 2013. However, farmers apply fertilizers trying to correct these deficiencies. In the low hills P availability may be constrained by low pH. The P in acidic forms is fixed mainly by hydroxides of Al and Fe more than remaining solubilized to be available for plants (Penn & Camberato, 2019). In the opposite situation, the alluvial plains show pH close to the neutral and near 6 times more CEC. These attributes may suggest a greater nutrient availability in the soil solution explaining its higher maize grain yield (Penn & Camberato, 2019; Sierra et al., 2003).

Agronomic management and maize grain yield

Regarding the effect of agronomic management on maize grain yield, for CS, we expected positive responses from plant density, total fertilizers, manual weeding, herbicides and insecticides on grain yield. However, only plant density increased the grain yield. The lack of fertilizer response was very surprising since farmers apply up to ~200 kg of NPK and soil P levels are low. We explored if the lack of response could be due a hidden interaction between the soil type and the cropping systems. For this, we plotted yield responses to NPK grouping by geopedologic units and cropping systems (Fig S7). In CS, we observed a slight positive response for both soil types, however, with high variability (Fig S7A). In TS, landraces did not show grain yield responses to NPK in the low hills and in alluvial soils fertilizers is almost not used (Fig S7B). Hence, this soil-cropping system interaction did not affect NPK on grain yield responses. We then, explored more deeply the diversity of fertilizer applications (Fig 9). In both systems, the diversity of fertilizers (different colours of pies) and the number (size pie) and timing of applications may have explained this high variability and the lack of response in grain yield. Our

results are consistent with those published by Njoroge et al., (2017) in tropical maize cropping systems in Kenia, Africa, where they found a strong spatial-temporal variation in grain yield across farms, seasons and fertilizer doses. Notwithstanding, comparable fertilizer x environment x genotype experiments such as those published by Kaizzi et al., (2012) showed more clear patterns in fertilizer doses and expected outcomes.

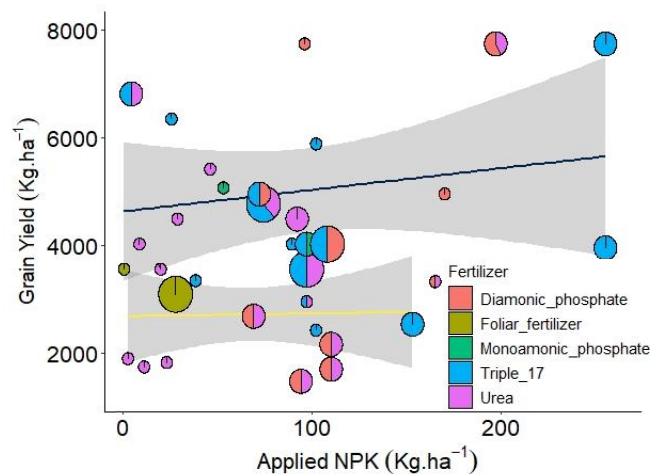


Figure 9: Grain yield (Kg ha^{-1}) responses as a function of total applied NPK (Kg ha^{-1}) in fertilizers grouped by hybrids (conventional systems, blue line) and landraces (traditional systems, yellow line). Each pie shows the percentage of the type of fertilizer applied and the pie size indicates the number of times the farmer applies it throughout the crop cycle (small pie, 1; medium, 2; large, 3 times of application).

Manual weeding and total herbicides were expected to be reduced in CS with higher plant density. Our results show that farmers who increased plant density decreased the herbicide use maintaining (or increasing) grain yield. Marín and Weiner, (2014) found that weed biomass is reduced from 7 pl m^{-2} of maize plant densities, onwards. Since CS explored a range from 2.5 to 9

pl m⁻² (Fig S4), higher maize plant densities may have reduce the weed pressure and herbicide use. Sikkema et al., (2008) found that increasing plant density in controlled experiments did allow reducing the herbicide input (till 50% of herbicides applications) without penalizing the grain yield. Plant density x weed pressure interaction emerge as a key management decision that may increase the sustainability and profitability of these systems. Moreover, in potential conditions maize hybrids have a curvilinear response to grain yield when plant density increases (Andrade et al., 1999). We found a linear positive response, suggesting that, at least for a same genotype, grain yield might be constrained by this driver (Fig S4). This result concord with those of small-scale maize farmers in Ethiopia that use sub-optimal plant densities (Seyoum et al., 2019). This suggest that maize low grain yield driven by low densities in small-scale contexts maybe constrained by inappropriate agronomic recommendations and or farmers' low purchasing power to buy seeds. A higher Plant density could not only reduce the herbicides use but also to increase grain yield (at least until reaching an optimum).

For TS we expected positive responses of plant density, fallow period, total fertilizers, insecticides and herbicides and a negative response of fire times on grain yield. No fertilizers nor insecticides effected grain yield and fire times and herbicides negatively affected grain yield. Contrary as expected, grain yield decreased with plant density (Fig S4). In the countryside the historical development and selection processes of landraces have been at low densities context. This is because maize has historically been sown intercropped with other species such as beans, chili pepper and pumpkins (Teran & Rasmussen, 1995). TS in MDC were maize monocultures. This mono-culturization and the desire of reaching higher yields by increasing landrace plant densities may have conducted to farmers to an agronomic management trap (following the

recommendations for maize hybrids). Maintaining traditional low densities may allow to farmers not only to obtain higher grain yield but also to re-incorporate the multi-crop system of “Milpa” (Nadal & Rañó, 2011). As expected, the fallow period and the fire times affected positively and negatively, respectively on grain yield. The above and below biomass accumulation in the fallow period serves as a source of nutrients that is slowly released to the crop during the ontogenic cycle instead of fertilizers in very soluble forms that may be adsorbed by hydroxides of Al and Fe in low hills (Ultisols) or leached and drained in alluvial plains (Entisols, (Penn & Camberato, 2019).

Neither in CS nor TS the amount of insecticides impacted positively on grain yield. These responses are not surprising since farmers may apply insecticides with a preventive strategy, this is applying with some frequency avoiding pest invasion or may apply with an adaptative strategy, i.e. knowing what pest is invading and applying when necessary. Both strategies may allow reachable grain yield however, the latter requires knowledge and monitoring but would reduce the insecticides use increasing crop system sustainability (Flores-Gutierrez et al., 2020). Finally, in both cropping systems increasing the use of glyphosate and paraquat decreased the grain yield. In México GMO resistant hybrids are prohibited but not the use of the technology-associated herbicides. Phytotoxicity effects associated to post-emergence applications appear to be a hidden factor reducing the grain yield in both cropping systems.

Underlying socioeconomic drivers related to maize cropping systems

We explored if some socioeconomic and cultural factors could influence agronomic decisions. Thus, we would be able to identify other motivations beyond technical rational decisions in

maize management. The birthplace and the prevailing maize cropping system relationship in Reforma Agraria and Barrio San Jose was clear. In these cases, it is likely that farmers are replicating their cultural background that they learned in their places of origin. Also, possibly due to family relationships within these communities, there is a greater degree of cohesion, social organization, which makes possible to build and strengthen networks of trust and reciprocity and the construction of a common meaning of maize management (collective learning; Muro and Jeffrey, 2008; Pahl-Wostl and Hare, 2004). Moreover, Zamora Pico de Oro showed that, peasants with multiple origins, kept their multiple cropping systems. The bigger size of *ejido* and lack of social cohesion may explain their prevailing diverse cropping system.

La Victoria and Quiringuicharo *ejidos* had different origins but showed a homogenization in the cropping systems. The construction of a determined knowledge includes social interactions and communication that individuals employ to create, use, and evaluate multiple types and sources of information (Swidler & Ardit, 1994). Thus, farmers coming from different places to an unknown region, may have found support in their neighbours' knowledge. This fact may have begun a process of construction of social capital, not evaluated in this study.

Conclusions and recommendations

The soil biophysical factor is a strong maize-grain-yield determinant regardless the maize cropping system. Moreover, fertilization strategies need to be better adjusted in relation to each soil type and type of maize cropping system. The agronomic tools derived from green revolution and the agronomic models that may have coherence and predictability in high-latitude cropping systems were not supported by field data in small-scale context in the Neotropics. This exposes

the necessity of developing new models identifying key drivers and functions of small-scale maize cropping systems. Furthermore, as there were not clear patterns in the amount and frequency of pesticide applications, we conclude that there is a very great potential to study the weeds and insects population dynamics and develop adaptive control strategies, rather than preventive ones in the maize cropping systems of the Neotropics. This could reduce agrochemical inputs increasing systems' sustainability. Finally, maize cropping systems are not totally developed by a rational basis. We highlight the importance of underlying socioeconomic and cultural mechanisms in the decision-making of maize cropping systems. Regards these previous knowledge could help of designing new theoretical models and concrete sustainable and suitable strategies in the tropical maize cropping systems.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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3.1 Capítulo 3: Figuras complementarias

Supplementary figures

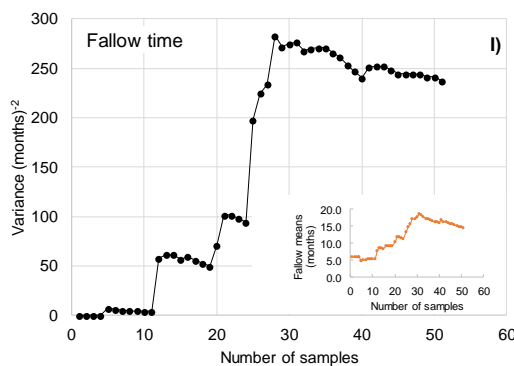
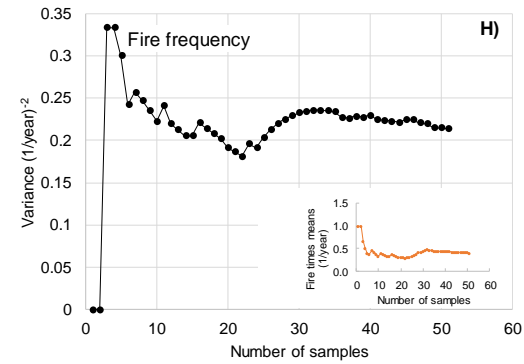
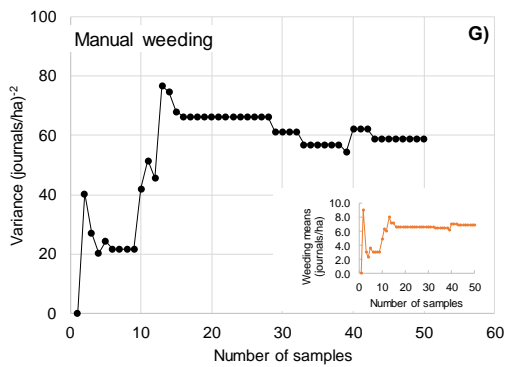
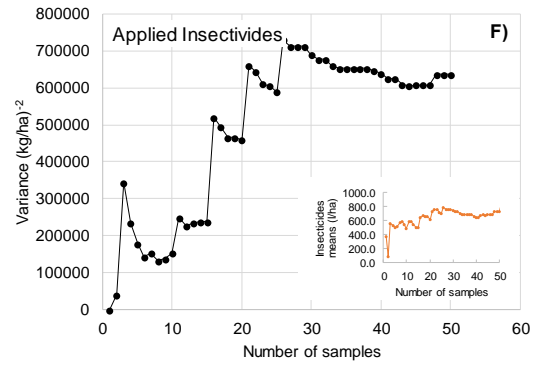
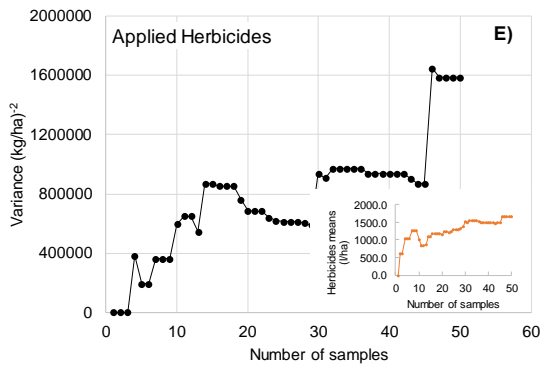
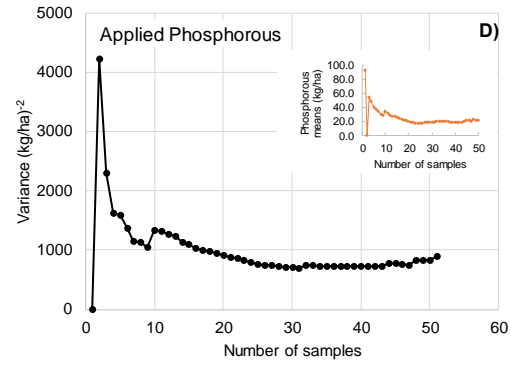
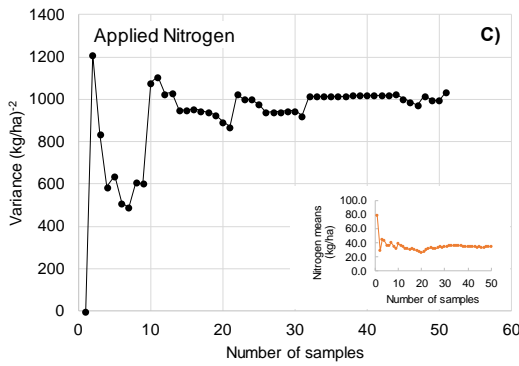
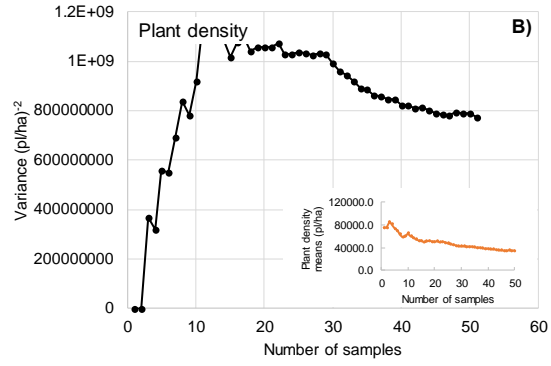
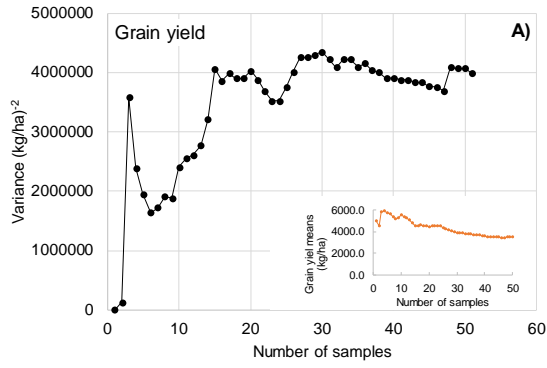


Figure S1: Cumulative variance (unit of the variable⁻²) vs. cumulative sample size (number of interviews) functions for the main agronomic variables incurred in maize cropping systems in the Neotropical region of Marqués de Comillas, Chiapas, México. A) Cumulative variance of grain yield, B) cumulative variance of plant density, C) cumulative variance of applied nitrogen, D) cumulative variance of applied phosphorous, E) cumulative variance of applied herbicides, F) cumulative variance of applied insecticides, G) cumulative variance of manual weeding, H) cumulative variance of fire frequency and I) cumulative variance of fallow period. Insets show the mobile mean of each variable.

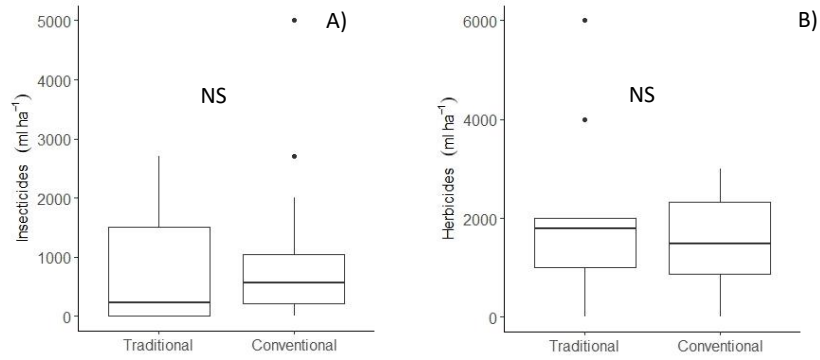


Figure S2: Box plots of total insecticides (A), total herbicides (B) in “Traditional” and “Conventional” maize cropping systems. These groups were separated by the use of the landraces (traditional) or hybrids (conventional). NS, no significant differences in ANOVA test.

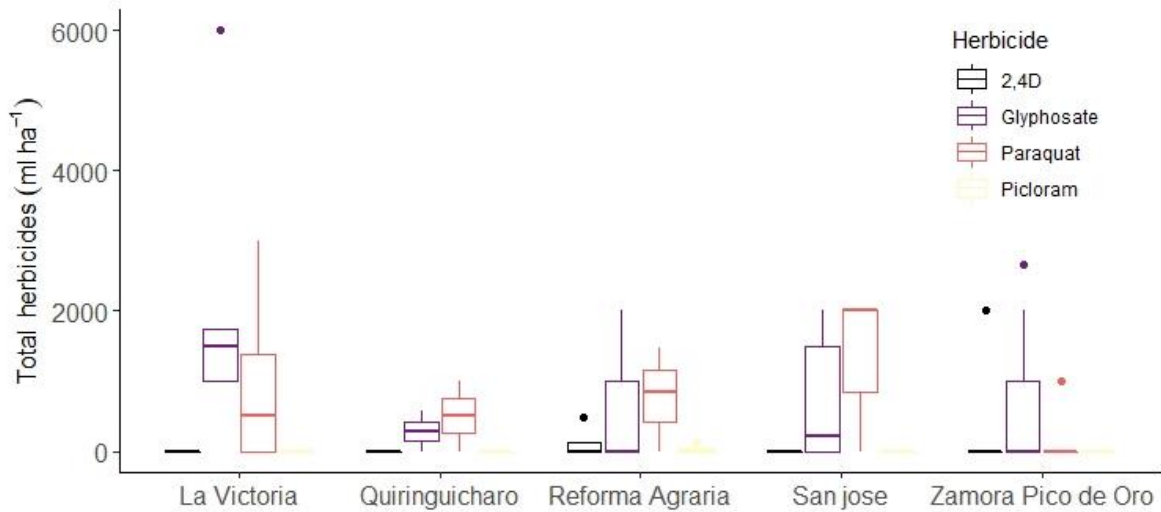


Figure S3: Box plot of Total herbicides used in the whole maize ontogenic cycle by farmers in each *ejido*. Glyphosate and Paraquat are the most used herbicides.

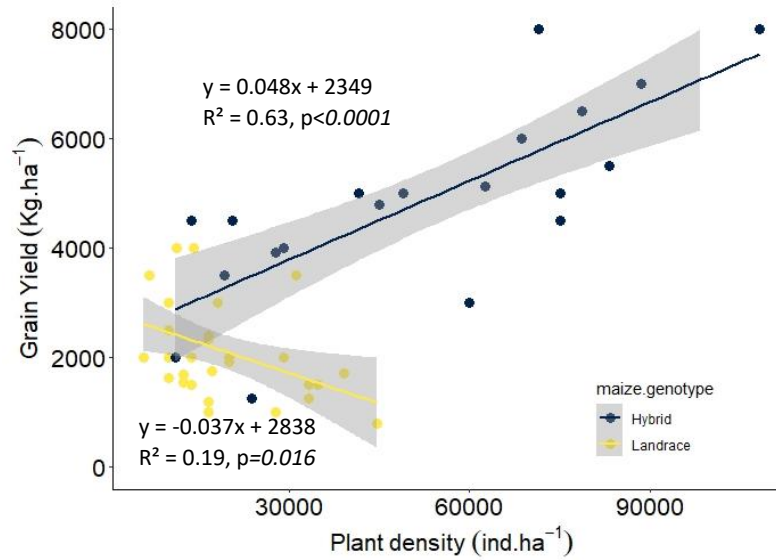


Figure S4: Grain yield (kg ha^{-1}) as function of plant density (ind ha^{-1}) for hybrids (conventional systems, blue points) and landraces (traditional systems, yellow points) in fifty-one farms in Marqués de Comillas region, Southwest México. For each linear regression, coefficients, p values and the R^2 are detailed. Grey area represents the 95% of confidence intervals.

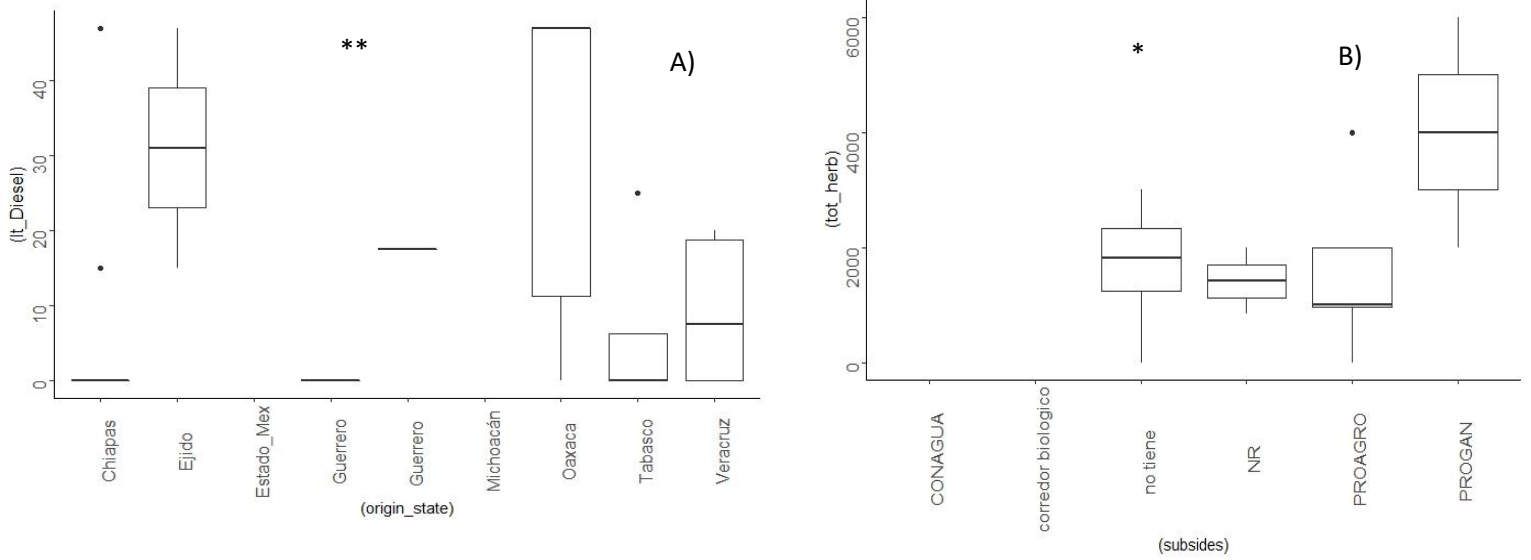


Figure S5: Significant relationships between socioeconomic and agronomic drivers. A) Boxplot of Liters of diesel incurred in mechanical labour and farmer birthplace. B) Boxplot relating the total herbicides (ml ha^{-1}) applied to maize cropping systems and the subsidies. p -values of ANOVA test are detailed. *: $p < 0.005$, **: $p < 0.001$ and ***: $p < 0.0001$.

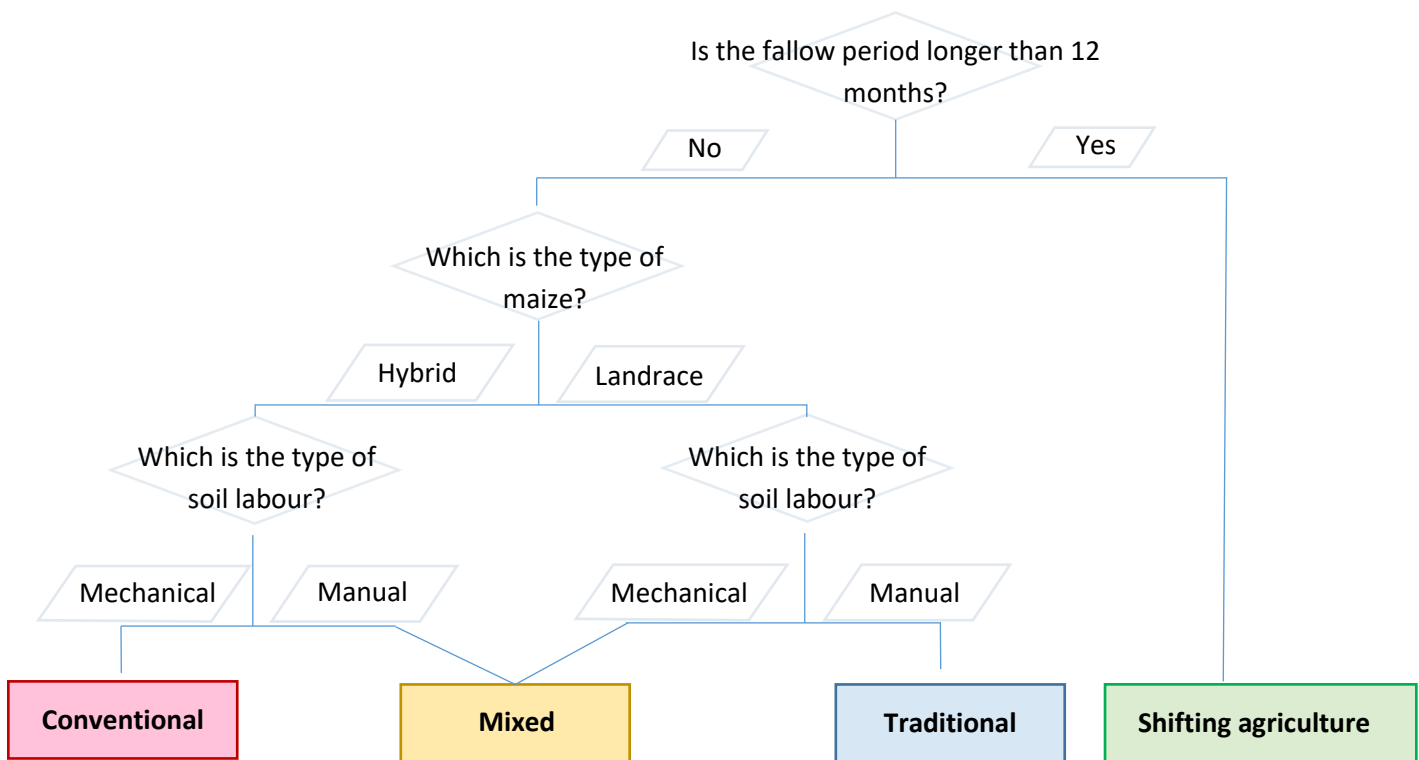


Figure S6: Decision tree diagram to classify the maize cropping systems. Diamonds represent the questions; parallelograms represent the answers. Squares represent the obtained typology of maize cropping system (colors are congruent to those in the alluvial graph, Fig 8).

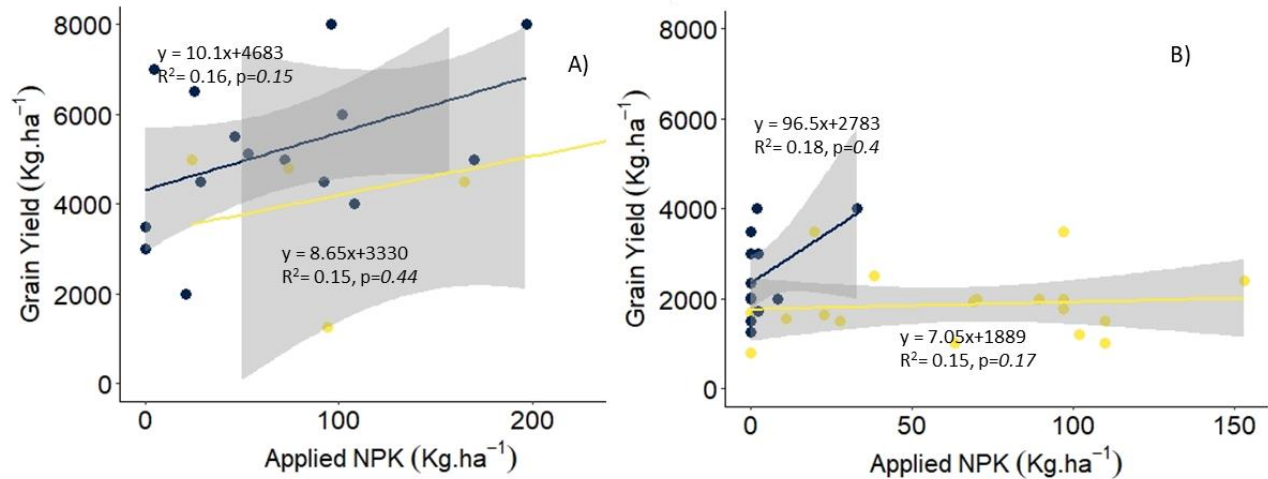


Figure S7: Maize grain-yield responses (Kg ha⁻¹) as function of total nutrients applied by fertilizers, NPK (Kg ha⁻¹) grouped by geopedologic units, alluvial plains (blue dots) and low hill (yellow dots) in Conventional A) and traditional B) cropping systems. For each linear regression, coefficients, p values and the R² are detailed. Grey areas represent the confidence interval (95%).

APPENDIX

Soil samplings

In each geopedologic unit, at least three plots were established to evaluate soil properties. In each plot, three composite samples were taken at 30 cm depth. Each composite sample consisted of six points distributed in a linear transect of 50 m with a separation of 7 m between transects. One soil pit (30cm deep) was dug randomly along each transect to take an undisturbed (100 ml) core sample for bulk density determination (n = 3 cores by plot), and to determine stone content in a pit wall (FAO, 2006).

Laboratory procedures and soil chemical analysis

In the laboratory, samples were air dried and sieved (< 2 mm) prior to analysis. Results are reported on a dry mass basis by correction for soil moisture content determined on sample

aliquots dried at 105 °C. The pH was measured in H₂O in the supernatant of a 1: 2.5 (wt:vol) soil suspension with an Aqua Lytic Senso Direct pH24 potentiometer. Total carbon (C) and Total nitrogen (N) were determined using a CHNS/O elemental analyzer (Perkin Elmer 2400 series II). Extractable phosphorus (P) was determined by the method of Bray-Kurtz and quantified by colorimetry (Van Reeuwijk, 1992). Exchangeable base cations (EC) were extracted with 1 N ammonium acetate buffered at pH 7. Exchangeable acidity (Hex plus Alex) was determined in 1 M KCl extracts by titration with 0.01 N NaOH and with 4 % NaF (H⁺), or by AAS (Al³⁺). The Al saturation (Al) in the cation exchange complex was calculated as follows:

$$\text{Al (\%)} = (\text{Al (cmol kg}^{-1}\text{)} / \Sigma (\text{Caex, Mgex, Kex, Naex, Hex, Al (cmol kg}^{-1}\text{)})) \times 100.$$

Soil texture was determined by the combined sieve and pipette method (Schlichting et al., 1995; Soil Survey Staff, 2011) after destroying organic matter with peroxide, dissolving CaCO₃ with diluted HCl, and dispersing the sample with sodium hexametaphosphate.

Capítulo 4: Optimización multiobjetivo para abordar la dicotomía de producir o conservar en sistemas agrícolas inmersos en paisajes tropicales modificados por humanos de alta biodiversidad

Artículo enviado a “Journal of environmental management” como:

Wies, Germán^{1*}; Groot, Jeroen C.J ²; Martinez-Ramos, Miguel¹ (2021). Strategies to overcome the conservation-production dichotomy in agricultural systems immersed in highly-biodiverse tropical landscapes should be highly context-specific to be successful.

Strategies to overcome the conservation-production dichotomy in agricultural systems immersed in highly-biodiverse tropical landscapes should be highly context-specific to be successful

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Abstract:

In humid tropics small and medium farming systems (TFS) are important for producing food but also because they already retain natural forest patches with high biodiversity. Forest conservation and agricultural production strongly compete for land in TFS. Finding solutions that synergize increasing conservation areas and agricultural production is an issue that has yet to be resolved in human-modified tropical landscapes. Achieving this goal demands including the large array of farm components and the multitude of interrelations among these components interacting with the conservation areas inside TFS. Pareto-based genetic algorithms that produce a set of solutions that satisfy apparent opposed objectives may tackle multi-objective problems. We explored trade-offs and synergies to increase the profits by sustainable intensification and at the

same time maintain or increase tropical rainforest areas in five TFS (SJ, LV, QU, RA and ZPO). There was a strong trade-off between conservation and economic profits in the five TFS. However, depending on the total farm area, initial configurations and the level of used external inputs, TFS showed low (SJ and LV) or high (QU, RA and ZPO) potential to increase forest conservation and profits. In SJ increasing conservation areas and profits was only possible through increasing external inputs mainly due to its small total farm area and intensification status. However, in QU, RA and ZPO farms it is possible to increase conservation areas and profits through sustainable intensification practises, such as increasing maize silage areas, changing high for low-pesticides use crops and plantations (beans and mahogany) but also decreasing variable cost through decreasing cost-supply uses (palm oil) or external feeds (*pollinasa*). Alternative management and resource allocation options were particular for each TFS. Hence, it is of paramount importance to consider singularities of farm context, configurations and management to overcome the conservation-production land competition.

1. Introduction:

Small and medium farming systems (<15 ha size) sustain more than 380 million farming households worldwide, they produce more than 70% of the food calories in the regions where they are present and are responsible for more than 50% of the food calories produced globally (Samberg et al., 2016). These farmers may be incentivised to change their land-use under the influence of cash commodities crops and the pressure of large-scale actors, and land tenure insecurity (Meyfroidt et al., 2014). Moreover, small family farmers face vulnerabilities due to

climate change with less resources to achieve innovation and actions for adaptation (Bouroncle et al., 2017; Donatti et al., 2019).

Tropical farming systems (TFS) have been developed in the most biodiverse regions in the world (Cincotta et al., 2000; William F. Laurance et al., 2014). Currently, in these regions there is a fast spread of simplified large-scale cropping systems (rice, soybean, palm oil and pastures for cattle) that threaten not only tropical rainforest (Ordway et al., 2017; Phalan et al., 2013) but also the diverse and multifunctional land-uses that are typical of peasants and indigenous traditional systems (Kass & Somarriba, 1999; Toledo et al., 2003). Monoculture expansion and intensification has put pressure to remove the remaining natural tropical patches inside the systems that still host species biodiversity and provide regulation and support ecosystem services such as water retention in streams, soil retention and fertility, biomass production and carbon stock (Alamgir et al., 2016; Melo et al., 2013; Muench & Martínez-Ramos, 2016).

To address these problems, the disciplines of conservation biology and agronomy have different approaches, which could be integrated. From the perspective of conservation biology, outside the protected areas there is a widely spread landscape configuration, recently defined as “Human Modified Landscapes” (HML, Melo et al., 2013). In HML small, medium and more recently big-sized farm systems co-exist. These still host old-growth forest fragments, and patches of second-growth forests (Chazdon et al., 2009; Gardner et al., 2009). One major constraint for conservation in HML is the advance of the agriculture frontier, which causes the loss, fragmentation, and degradation of forest habitats (Taubert et al., 2018; Tyukavina et al., 2015). On the other hand, TFS face an important challenge of producing food for farmers’

families and for society, maintaining the systems' complexity and multi-functionality without threatening the still present tropical rainforest patches that sustain tropical ecosystem functions and services (Melo et al., 2013; Pinillos et al., 2020).

To integrate forest conservation and sustainable food production in TFS, the first challenge is to explore alternative land-uses and management practises, which increase farm productivity and economic profits while maximizing primary or mature forest patches inside farms. As many TFS are characterized by economy of subsistence with low investment in technology and limited access to financial support (Donatti et al., 2019), an agronomic approach should guarantee productive and economic development while not involving large investments or expenses that farmers cannot afford (Kanter et al., 2018). A sustainable intensification approach may include agroecological practices, diversified cropping systems, nature mimicry, and some forms of conservation agriculture and of agroforestry (Pablo Tittonell, 2014). Traditional farming systems (e.g. shifting agriculture) may also be valuable. Major and widely applicable adjustments implemented in the context of sustainable intensification may include decreasing external inputs (pesticides, fertilizers and external feeds) and increasing crops diversification and farm self-resilience (Cortez-Arriola et al., 2016; Flores-Sánchez et al., 2015).

In systems involving productive and environmental objectives while meeting farm and conservation constraints, interactions among objectives may behave as trade-offs or synergies. The use of tools that enable farm re-configuration and providing insight about the interactions between these objectives would be important to inform farmers and stakeholders about potential adjustments to be implemented. Simulation models have been developed to tackle this issue at

the farm, landscape and regional levels (Chopin et al., 2015; Groot et al., 2012; Todman et al., 2019). A particular group of these models are based on multi-objective optimization algorithms that generate a large set of Pareto-optimal alternative farm configurations characterised by adjusted management and resource allocation that satisfy the required initial conditions. Such models depart from the original farm configuration and generate a set of alternative solutions satisfying the constraints initially established. The Pareto ranking procedure selects solutions that better perform compared to the initial situation. The improvement process of alternative solutions mimics the models of the process of natural selection. This process is repeated until all solutions are assigned to an optimized Pareto rank (detailed description of the algorithm procedure can be found in Groot et al., 2012).

Particularly, in México multi-objective models have been applied to dairy systems for sustainable intensification (Cortez-Arriola et al., 2016; Val-Arreola et al., 2006) and to maize-livestock systems to improve income, labour input and soil organic matter (Castelán-Ortega et al., 2003; Flores-Sánchez et al., 2015). However, they have not been applied in systems that require finding options to optimize agricultural production and conservation of rainforest. Moreover, these models, although they have been applied in systems for managing natural resources and production (Groot et al., 2007, 2010; Groot & Rossing, 2011; Todman et al., 2019), they have never been applied in areas where tropical rainforests have a strong pressure to be cleared. This approach may not only provide alternatives that reconcile objectives, but also provide an alternative approach and insights for the *land sharing vs. land sparing* framework (Baudron et al., 2021; Fischer et al., 2014).

The objectives of this study were i) to explore trade-offs and synergies aiming to increase the profits by sustainable intensification and at the same time maintain or increase tropical rainforest areas inside TFS, ii) to investigate the management and land-use configurations determining alternative solutions in the simulation outcomes, and iii) to compare how different TFS with contrasting farm characteristics have different solution spaces. We based our study on five farm systems of different communities in Marqués de Comillas region, state of Chiapas, Mexico, a highly biodiverse humid tropical region where a fast migration process resulted in a rich diversity of farm systems which still host different proportions of tropical rainforest patches inside the farms (Zermeño-Hernández et al., 2016).

2. Materials and methods:

2.1 Study region (Case of study):

Marqués de Comillas region (MDC) (16°54'N, 92°05'W), Southeast México (Fig. 1) covers an area of ~2,008 km². The mean annual precipitation is ca. 3000 mm with a dry season of two months (February-April less than 60 mm month⁻¹) and with a mean monthly temperature of 22°C (Martínez-Ramos et al., 2009). Before 1970, MDC was totally covered by old-growth forest. Then, MDC was part of the land distribution program of the Mexican federal government (Tarrío García & Concheiro Bórquez, 2006). The region experienced immigration from different states of Mexico. Many groups of peasants and indigenous people from different states (Chiapas, Guerrero, Jalisco, Michoacán, Oaxaca, Tabasco) and also Guatemala (de Vos & Marion, 2015) arrived to start or continue their farming activities. These groups were lumped in “*ejidos*”,

communities with a relative degree of political and institutional organization and autonomy (Alcorn & Toledo, 1995). In each *ejido*, the land distribution is determined collectively but also, the whole group decides whether they administrate the communal lands. In many cases communal land is for forest conservation and/or eco-tourism (Alcorn & Toledo, 1995).

Federal incentives during the 1970-80's promoted cattle ranching pastures and staple cropping and more recently palm oil production (Julia Carabias et al., 2015; Castellanos-Navarrete & Jansen, 2015). Currently, ~70% of the region is covered by agricultural land-uses such as maize, beans, chile and palm oil crops; pastures for cattle and secondary and old growth forest patches (Zermeño-Hernández et al., 2016). However, as the *ejidos* are mostly constituted by people with the same place of origin and are therefore rather homogeneous, the differences between *ejidos* are large as reflected in different agricultural production characteristics associated with the customs of the inhabitants (Wies et al., 2020, submitted).

2.2 Interviews and farming systems characterization

Sixty-two interviews were performed in the MDC in five *ejidos* with different origin groups. At least eleven interviews were performed in each *ejido* representing >9% of total farmers of the sample and 9.5% of the total area of the *ejidos*. To characterize the TFS we designed a semi-structured interview aiming to describe the whole farm land-uses and main drivers and farm functioning incurred (see the interview in Appendix 1). The most frequent land-uses in farms were maize cropping, cattle ranching and remaining forest areas followed by bean cropping, palm oil and maize cropping for silage (Fig. S1 and Table S1). The most typical

management for cattle production was free grazing in pasture paddocks complemented with some additional feed (maize grain, maize silage or chicken manure “*pollinasa*”) depending the amounts on the cattle land-use extent and stocking rates i.e. depending on the level of cattle ranching intensification. For each crop or plantation, we asked the main drivers incurring the inputs and outputs. We also registered other management practices such the fallow period, fire times (i.e. fires induced before sowing for clearing secondary vegetation grown in the fallows) and crop rotations. When we visited the farmers and carried out interviews, we toured the countryside together with the farmer while asking the questions. This tour served us to visually check the information they were providing (e.g. type of insecticide and amount) and to georeference the vertices of the farm to check the extents they indicated. As farmers answered in different units or quantities they were familiar with (e.g. number of bottles of used insecticides) when necessary, quantitatively recorded variables were recalculated in common units (e.g. from bags of fertilizer to kg N ha^{-1}). Similarly, for agrochemicals, we registered the brand and then calculated the amount of active ingredients applied.

Model-based farm construction. For each community we modelled a typical farm in the whole-farm bio-economic model FarmDESIGN (Ditzler et al., 2019; Groot et al., 2012). First, we counted current activities in farms grouped by *ejido*. We considered activities practiced by five or more farmers (Supplementary Material, Fig S1). Land-uses for each typical farm are shown in Table S1. Inputs, outputs and management decisions for land-uses are detailed in Figure S2. For the cattle production activity, we collected data pertaining to herd structure, meat production, body weight, dry matter intake (DMI), labour input, and sanitary and reproductive management. For the cropping activity, we collected inputs (seeds, fertilizers, herbicides and insecticides) and

outputs (grain or fruit yields and estimated manure). Also, we registered forage species and utilization (to estimate grass productivity) and labour, costs, subsidies and allocation. For cattle production activity, some variables were estimated or obtained from the literature. Parameters to estimate DMI capacity, metabolizable energy (ME) and crude protein (CP) requirements per animal type in the herd were obtained from NRC standards (NRC, 2001). Nutrient requirements for maintenance, growth and meat production were obtained from NRC (2001), as well.

2.3 Data analysis

Description of the model. To explore trade-offs or synergies between development objectives as influenced by choices on agricultural land-uses and conservation areas we used the FarmDESIGN model. This simulation model quantifies farm production, nutrient flows and cycles and economic profits (Groot et al., 2012). We used the initial typical farms information to generate alternative farm configurations that could optimize conservation and production. The model uses an evolutionary algorithm to generate alternative configurations of agricultural production systems by adjusting land-use areas and inputs (crops, animals, manures, fertilizers, herbicides), and evaluating the indicator responses related to production, economics and conservation.

Inputs required for the model describe the biophysical environment, socioeconomics (production costs for activities and labour), type and crop products (agronomic inputs and outputs), herd composition and products (production costs and outputs), manure types and degradation rates, external sources of mineral nutrients (through animal food or fertilizers) and

physical assets. A static farm balance model calculates a large range of indicators pertaining to nutrient and organic matter flows and balances, herd feed consumption and energy and protein balance, the manure balance, labour balance and economic results. The model can be freely downloaded from <https://fse.models.gitlab.io/COMPASS/FarmDESIGN/>.

For the exploration, management drivers or inputs were considered “decision variables” which have to be set within coherent ranges. Also constraints for farm functioning must be set. Outcome variables can serve as objectives that can be either minimized or maximized.

Decision variables. In our study, crops (including pastures for cattle) and forest areas, agrochemicals (fertilizers and pesticides) and were considered. Moreover, decision variables were added to modify the destination of products, such as maize grain from crop to feed animals or self-consumption (Table 1).

Constraints and objectives. Adjustments in decision variables lead to changes in model outcomes. Outcomes can be selected as constraints that should be within a given range, or as objectives that can be minimized or maximized. Important constraints relate to the feed balance: the deviation between demand and supply of energy and protein should be within narrow ranges to allow the production levels to be defined by animal numbers and corresponding productivity. Moreover, the dry matter (DM) supply to the animals cannot exceed the intake capacity. Another important constraint was the maximum conservation area which could not exceed the total farming area. Minimum area for maize and beans required for self-consumption was also specified. An overview of selected constraints and their allowed ranges for farm in La Victoria is presented in Table 1 (see variables and constraints information of completing farms in table S3).

Table 1: Decision variables and constrains set for the multi-objective optimization for the typical farm in *ejido* "La Victoria".

		Decision variable	Initial	Minimum	Maximum
<i>Variables</i>	Land-use areas	Rainforest area (ha)	16.19	0	63
		Maize (ha)	1	0.5	10
		Beans (ha)	1	0.5	3
		Palm oil (ha)	24.5	0	63
		Lemon (ha)	2	0	5
		Permanent pastures (ha)	16	5	63
		Mahogany afforestation (ha)			
		Fruit trees (ha)	1	0	2
		Fertilizers	Triple 17 (kg)	8282.5	0
	Urea (kg)		354	0	1000
	Pesticides	Cypermethrin (l ha ⁻¹)	0.75	0	4
		Paraquat (l ha-1)	65.55	0	1000
		Chlorpyrifos (l ha-1)	4.591	0	10
		Glyphosate (l ha-1)	73.3	0	1000
		Lufenuron (l ha-1)			
	Feed for cattle	Maize grain (kg)		0	25000
		Pollinasa (kg)		0	25000
<i>Constraints</i>	Land-use areas	Farm area (ha)	61.5	60	62
		Cropping area (ha)	29.5	1	61
		Cattle production area (ha)	16	1	61
		Conservation area (ha)	16	0	61
	Feed balance	Saturation (%)	-22.9	-999	0
		Energy (%)	-3.6	-5	5
		Protein (%)	39.5	0	45

Finally, we selected six common objectives for the five farms. Following the research question of the study, the main objectives were maximizing the economic profits (considered as

an integrator of total agricultural production) and the conservation forest areas. Then, agricultural production had to include sustainable intensification practises as alternative managements that allow an easier transition for improvement in smallholders farming systems. The common objectives for all TFS were:

- Maximizing economic profits
- Maximizing forest conservation areas
- Maximizing the feed protein self-supply
- Maximizing the land-use evenness
- Minimizing agrochemical use (herbicides, insecticides)
- Minimizing variable costs.

2.4 Statistical analyses and software

We used R software (<http://www.R-project.org/>) and RStudio (<http://www.rstudio.com/>) interface for data analysis. In particular, “FactoMiner” package was used for principal component analyses (Lê et al., 2008) and “Tidyverse” for plotting (Wickham et al., 2019).

3 Results

3.1 Trade-offs and synergies objectives exploration and farm-configuration associated drivers

Figs. 1 and 2 show the relations among the six objectives for the San Jose (SJ) and La Victoria (LV) farms, and principal component analysis (Fig. 3) indicates the relations between decision variables and objectives. In SJ, there was a trade-off between forest conservation and economic profits (Fig. 1K and Fig. 3A). The latter was driven by larger maize areas associated to higher pesticides use (Fig 3A). Also, there was a synergetic relation between minimizing variable costs (driven by the *pollinasa* external feed, Figs 1A and 3A) and maximizing protein self-supply which was associated to an increase in pasture area (Figs 1D-F and 3A). Solutions with larger pasture areas therefore had lower variable costs (Fig 1A) and consequently higher profits.

Increasing land-use evenness would require a reduction in pasture area and an increase in *pollinasa* imports leading to higher variable costs and lower feed self-supply (Figs 1B-C). The original situation for pesticides appeared in the optimized frontier (Figs 1G-J), positively driven by maize areas (increasing pesticides pressure) and negatively by forest areas. Synergetic improvements relative to the original situation that reduced variable costs, and increased land-use evenness, protein self-supply and forests areas were found with intermediate pasture areas (~15 ha) and low *pollinasa* use (Fig 1, solutions between black lines).

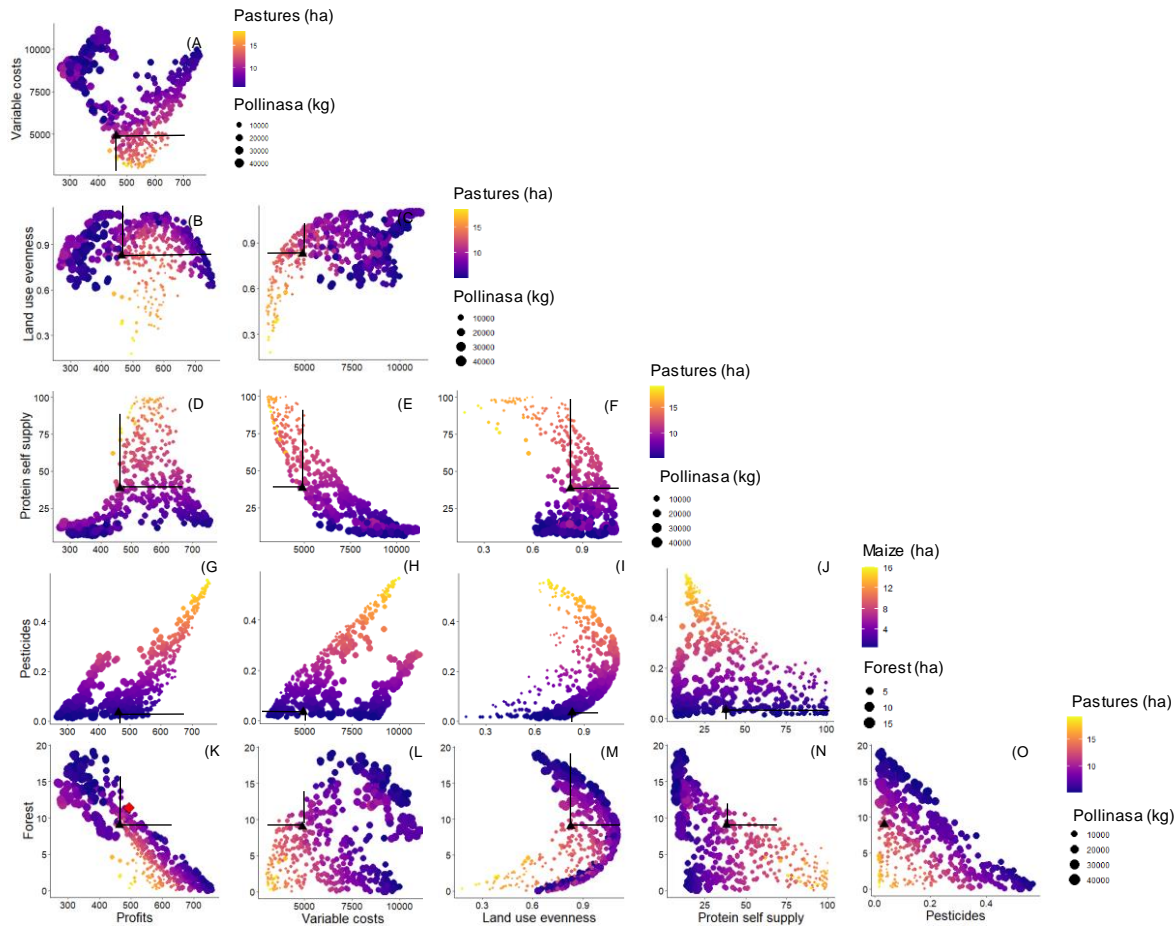


Figure 1: Relations between optimization objectives for San Jose farm. Each dot represents one alternative solution resulting from optimization. Triangles denote the farm initial situation. The black lines represent synergic improvement relative to the original situation. For each objective in Y-axis the two most correlated farm drivers (variables) are detailed with colours (first correlated) and dot size (second correlated).

In La Victoria farm (LV), there was a trade-off between economic profits and forest areas too (Fig. 2 K). Increasing palm oil areas determined higher economic profits but with higher variable costs associated to higher pesticide use (Figs 2A, 2G and 3B). On the other hand, higher

land-use evenness, forest areas and the protein self-supply could be reached by decreasing palm oil and increasing the pastures areas (Figs 2B-F, 2K and 3B).

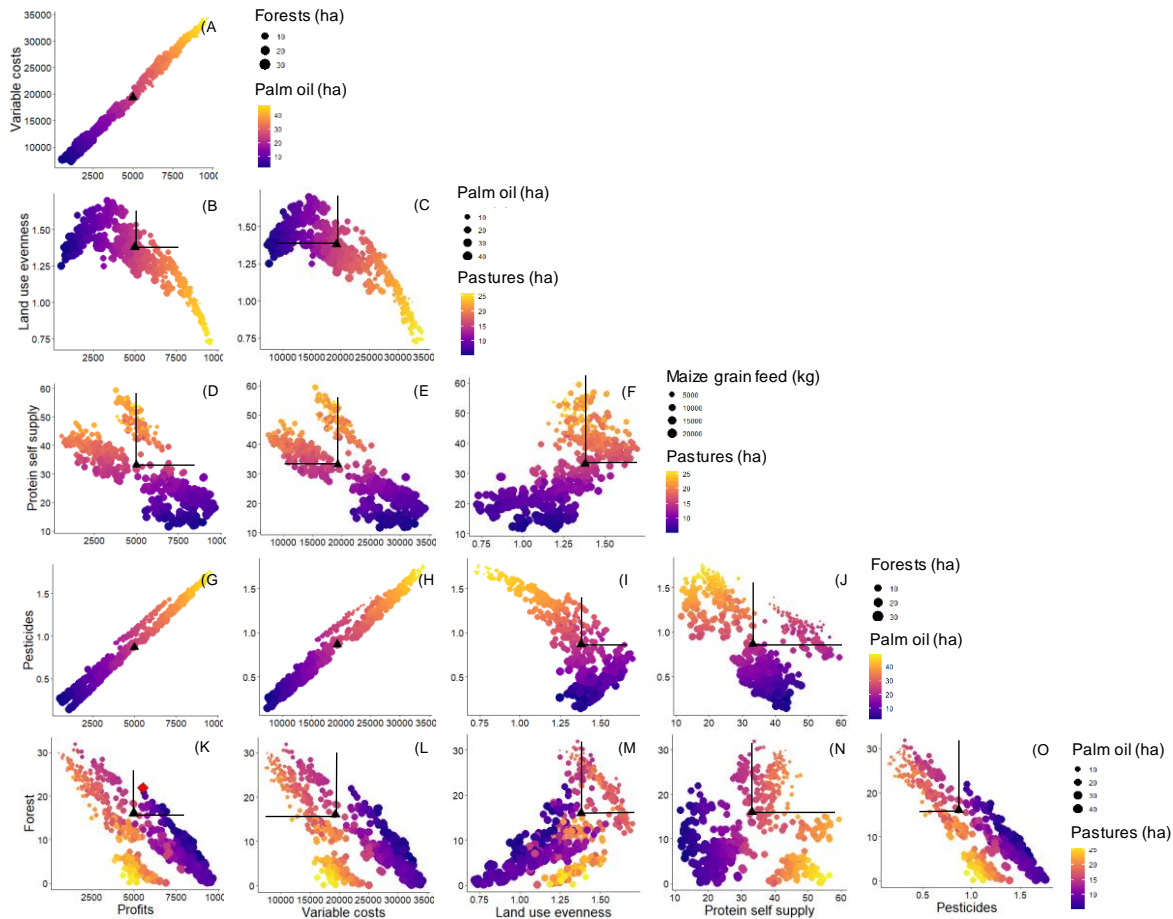


Figure 2: Relations between optimization objectives for La Victoria farm. Each dot represents one alternative solution resulting from optimization. Triangles denote the farm initial situation. The black lines represent synergic improvement relative to the original situation. For each objective in Y-axis the two most correlated farm drivers (variables) are detailed with colours (first correlated) and dot size (second correlated).

In Quiringuicharo farm (QU), economic profits positively correlated with greater maize and beans areas, but negatively with forest, pastures and land-use evenness. In this farm, no pesticides were used and all protein in animal feeds were produced on the farm therefore pesticides use was equal to zero and protein self-supply was full covered (Fig. 3C). The original farm configuration showed a great potential for maximizing economic profits and increasing forest areas for conservation (presumably due to its large total extension, Figs 3C and S2). For Reforma Agraria (RA) farm, economic profits correlated positively with greater beans areas and land-use evenness, and negatively with forest areas (Figs 3D and S3). Higher variable costs correlated with higher pesticides use in the maize crops and negatively with increasing pastures (Figs 3D and S3). Though the protein self-supply was satisfied (100%) in this farm, by increasing maize silage areas, it would be possible to decrease variable costs to increase economic profits (Fig. S3D and S3K). This farm showed a great potential to increase forest areas by decreasing beans and increasing maize silage areas (Fig. S3K).

In Zamora Pico de Oro farm (ZPO) the trade-off between pastures and *pollinasa* (Figs S4A-F) drove variable costs, land-use evenness and protein self-supply. When increased pastures areas, it increased the protein self-supply. When increased the *pollinasa* feed, increased land-use evenness but also, variable costs. Palm oil and maize areas were positively correlated with pesticides (Figs S4G-J and 3E). Finally, there was a trade-off between forest areas and economic profits. Profits were positively correlated with increasing mahogany and palm oil areas and higher pesticides use (Figs S4K-G and 3E).

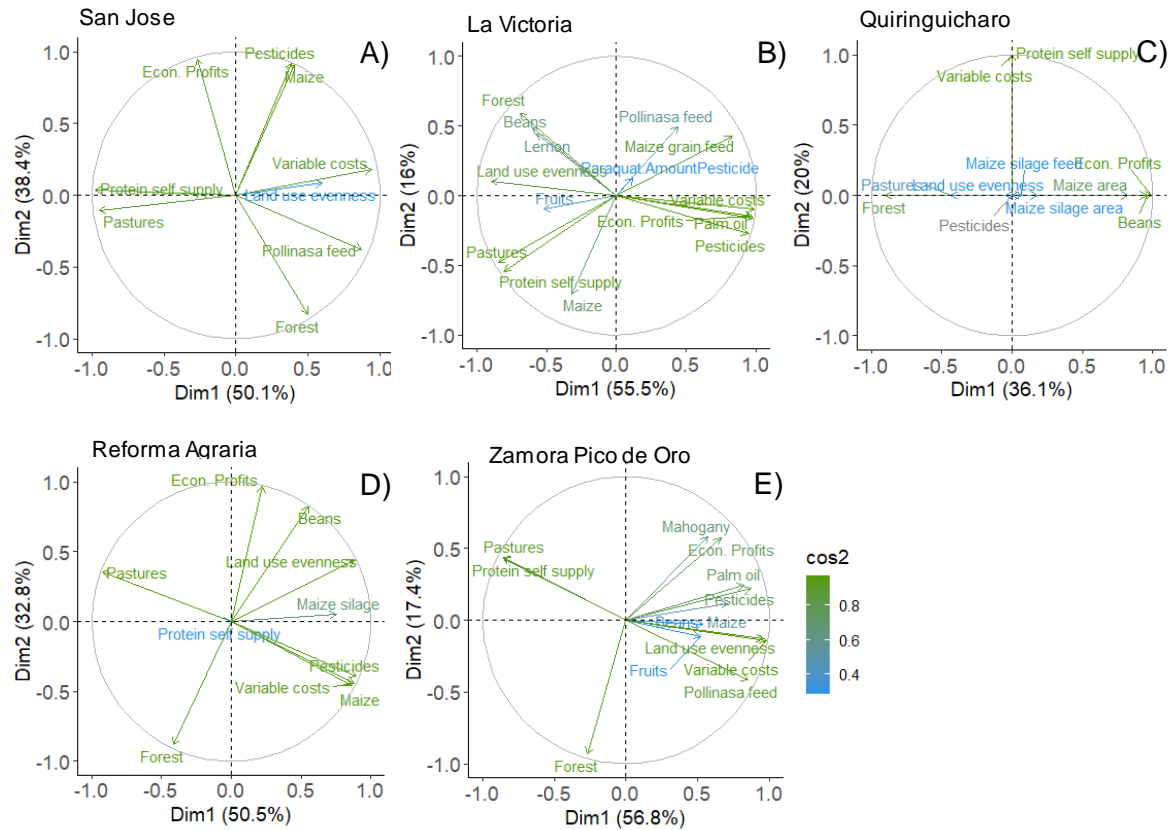


Figure 3: Correlation plot from the PCA analysis for five farms in MDC region, Chiapas, México. Arrows represent objectives (economic profits, forest areas, pesticides, protein self-supply, land-use evenness and variable costs) and management variables (crops areas, maize, palm oil, beans, pastures, mahogany and feeds, maize grain, pollinasa and maize silage). The greener variable the better well represented by the dimension 1.

3.2 Analysing the initial situations and those optimized in the conservation-production trade-off frontier

Relative to the initial farm situations, the options to simultaneously improve forest conservation and profitability differed between TFS. Both low and high income TFS showed low and high potential to increase conservation areas and/or increase economic profits (see the

distances between black triangles with red diamonds in Figs 1K, 2K, S3K, S4K, S5K and Table 2). For TFS with low potential, improving the conservation-production dichotomy meant a penalization in sustainable intensification objectives such as decreasing protein self-supply (19% and 51.5% for SJ and LV) and increasing variable costs (~15% for both, Table 2). It is necessary to highlight that in SJ, a low-income farm, the total volume of pesticides used is only ~10% of the application in LV because the smaller land size (24.0 vs 61.5 ha) and the livestock-traditional maize system in SJ compared to livestock-palm oil with high input rates in LV.

TFS with high potential for conservation and production i.e. QU, RA (similar to QU and therefore not included in Table 2) and ZPO showed that increasing conservation areas and increasing economic profits simultaneously could be achieved through maintaining or improving the sustainable intensification objectives. For QU (low income), increasing maize, maize for silage (2.4 to 13 ha, table 2) and beans areas could increase in crop diversity and economic profits twofold while pastures areas could be released for conservation (53 to ~2 ha, table 2). A larger amount of maize silage feed could compensate the reduction in pasture area resulting in maintaining protein self-supply (Table 2). In high income TFS of ZPO decreasing the palm oil area by 86% and increasing mahogany area ~3.9 times (high value afforestation) may enable an increase of ~56% in conservation areas and economic profits. Moreover, palm oil production reductions would decrease pesticide use and variable costs (Table 2).

Table 2: Areas (ha), management variables and sustainable intensification objectives for TFS that have low (San Jose and La Victoria) and high (Quiringuicharo and Zamora Pico de Oro) potential to improve conservation areas and economic profits. San Jose and Quiringuicharo farms represent low-income farms and La Victoria and Zamora Pico de Oro represent high-income farms.

		Low income			High income			
		San Jose (SJ)			La Victoria (LV)			
		Current	Improved		Current	Improved		
Low potential to improve	Areas	Fruits				1.0	0.5	↓
		Beans				1.0	0.7	↓
		PalmOil				24.5	26.3	↑
		Lemon				2.0	2.9	↑
		Pastures	13.0	9.3	↓	16.0	6.9	↓
		Forests	9.0	11.4	↑	16.0	21.9	↑
		Maize	1.0	3.8	↑	1.0	0.9	↓
	Variables	Maize grain feed				9500.0	19755.3	↑
		Pollinasa	14908.9	14641.5	≅	14000.0	12724.5	↓
		Triple 17	150.0	31.1	↓	8282.5	7312.1	↓
		Urea	200.0	275.2	↑	354.0	402.6	↑
	Sustainable intensification objectives	Pesticides	0.0	0.1	≅	0.9	1.0	≅
		Proteins self-supply	38.2	31.1	↓	33.2	17.1	↓
		Shannon	0.8	1.0	≅	1.4	1.3	≅
Variable costs		4902.2	5647.7	↑	19310.7	22038.4	↑	
		Low income			High income			
		Quiringuicharo (QU)			Zamora Pico de Oro (ZPO)			
		Current	Improved		Current	Improved		
High potential to improve	Areas	Fruits				1.5	0.9	↓
		Beans	0.8	15.5	↑	1.0	1.0	
		PalmOil				11.0	1.5	↓
		Lemon						
		Pastures	53.0	1.8	↓	48.5	44.6	↓
		Forests	13.0	25.7	↑	14.5	22.6	↑
		Maize	0.6	12.7	↑	3.0	1.5	↓
		Maize silage	2.4	13.0	↑			
		Mahogany				2.0	7.7	↑
	Variables	Maize grain feed						
		Maize silage feed	9957.2	14818.0	↑			

	Pollinasa				30675.9	31049.6	≅
	Triple 17				1423.0	1276.0	↓
	Urea				336.0	907.2	↑
Sustainable intensification objectives	Pesticides	0.0	0.0	=	0.2	0.1	≅
	Proteins self-supply	100.0	100.0	=	62.7	60.4	≅
	Shannon	0.7	1.4	↑	1.2	1.2	=
	Variable costs	2140.0	2140.0	=	7590.4	5902.6	↓

4 Discussion

4.1 Strategies associated to the trade-off between conservation and agricultural production

We explored potential alternative farm configurations and management strategies in TFS that could contribute to maximizing conservation areas and sustainable intensification production. The trade-offs between producing obtaining higher profits versus conserving forest were clear across all TFS (Figs 1K, 2K, S-6). However, farm modelling using Pareto-based multi-objective optimization yielded alternative solutions that could be applied to increase conservation areas and increase incomes ameliorating the local pressure of agricultural expansion on the still pristine tropical rainforest.

Regarding objectives and decision variables, for all farms, the objective of increasing forest areas was not directly related with some land-use area or management (only for LV, forest areas correlated with beans and lemon areas, Fig. 3B). On the other hand, increasing economic profits was associated with particular crops/managements, depending on each TFS configuration (Fig. 3). Hence, conservation and production objectives seem to be reachable through increasing the unit of product per area, this means intensifying the production areas. Initial farm

configurations determined the possibility of intensifying through increasing external inputs (e.g. in SJ, see below) or through sustainable practices (e.g. in QU, see below).

Our study shows that increasing production and conservation it is possible for all studied TFS, however, it depends on the initial situation of each TFS, specifically the total area, land-use configurations and external inputs. For example, for SJ improving conservation-production objectives depended on increasing variable costs in external feeds (pollinasa). In contrast, for LV, to increase production and conservation it would be necessary to reduce variable costs and external feeds through decreasing palm oil areas and increasing pastures. Unlike SJ and LV, in QU it would be necessary to increase beans, maize, and maize for silage areas to increase profits while pasture areas could be released for forest. In RA the strategy of releasing pastures areas for forest concomitantly with increased maize silage areas would result in lower variable costs and as a consequence increased economic profits. Finally, for ZPO improving conservation and production objectives would be mainly driven by decreasing palm oil, which would be associated with decreased variable costs and would allow Mahogany afforestation.

4.2 Multi-objective optimization for conservation-production issues

For natural resource management and production Groot et al. (2010, 2007) applied the Landscape IMAGES model to spatial planning to reconcile crop yields, nutrient losses and natural hedgerows structure. One important result was that for improving hedgerow cohesion it would be necessary to replace longitudinal to transversal hedgerow positions incurring new costs of implementation. In our case, for those farms which had more potential to increase forest areas

(QU, RA and ZPO), fragments could be established strategically in the systems to, for example, reduce erosion in plots with high slopes or leave streams covered to prevent them from drying out (Grimaldi et al., 2014). Strategic allocation of forest regeneration patches does not require financial investment and could increase long-term returns by conserving natural resources.

Todman et al. (2019) evaluated agricultural landscapes with different crop managements and their potential negative impacts on the environment (greenhouse gas emissions) with a multi-objective optimization algorithm coupled with a crop production model (NSGA-II with Rothamsted Landscape model). They found that in the best soils (expected to produce high yields) management strategies still have a great potential to improve environmental and economical outcomes although these results were counterintuitive and good for discussion amongst stakeholders. Similarly, we found alternative configurations for leaving forest patches despite the strong trade-off between forest areas and economic profits. Also multi-objective simulation highlighted different land use practices for each farm that could increase economic profits per hectare releasing areas for forest.

4.3 Contributions to the *land sharing* vs. *land sparing* debate

Various studies have provided theoretical and practical support to the idea that increasing yields per hectare is an effective tool to release land for conservation (*Land sparing* approach, Folberth et al., 2020; Phalan et al., 2016, 2014, 2011). On the other hand, there are studies that show that simplified-high yield crop systems are the main causes of tropical deforestation (Byerlee et al., 2014; Meyfroidt et al., 2014; Richards et al., 2012; Wassenaar et al., 2007).

For a land-sparing strategy to be successful in our case study, TFS with higher input uses, higher production and higher economic benefit should have allowed a larger proportion of forest areas. However, in contrast, TFS with the highest income per hectare and highest pesticides use (Table 3, LV and ZPO) showed low percentage of forest cover (the lowest for the case of ZPO) compared to those TFS with the smallest areas (SJ and RA with 24 and 43.5 ha, respectively) and intermediate economic profits per ha (Table 3). These relatively small TFS with low pesticides use showed the largest proportions of areas under conservation. Hence, *land sparing* in human modified tropical landscapes with high yielding activities (using high external inputs) may produce high economic incomes but not guarantee the forest conservation. Moreover, these activities lead to dominance of monocultures and increased pesticides use and associated negative externalities for the environment.

Table 3: Core indicators of production and conservation in the Tropical farming system (TFS) of San Jose (SJ), La Victoria (LV), Quiringuicharo (QU), Reforma Agraria (RA) and Zamora Pico de Oro (ZPO) farms in Marqués de Comillas region, Chiapas, México.

Farm	Total pesticides (ml ha ⁻¹)	Economic profits (US\$.ha.yr ⁻¹)	Proportion of forest (%)	Total farm area (ha)
SJ	2.6	462.9	37.5	24.0
LV	13.5	4998.9	26.0	61.5
QU	0.0	112.9	18.6	69.8
RA	2.5	74.7	46.0	43.5
ZPO	5.8	3083.3	17.8	81.5

4.4 Multi-objective optimizations in Mexican farming systems

Few studies in Mexico have been performed with multi-objective models to evaluate alternative solutions in farming systems. Flores-Sánchez et al. (2015) evaluated alternative solutions with FarmDESIGN in smaller farms (1 to ~4 ha) in Guerrero state. Unlike our study, authors simulated new alternatives (fertilization and soil endowments and animal husbandry) to evaluate *ex-ante* improvements in farms' economy, soil conditions and labour. Cortez-Arriola et al. (2016) using FarmDESIGN applied comparable principles of sustainable intensification (maximizing gross margin and organic matter balance and minimizing feed costs, labour balance and nitrogen balance) to six typical dairy farms in Michoacán state. They found synergies between increasing economic incomes and decreasing feed costs. Similarly, LV and ZPO farms showed negative correlations between external feeds (maize grain or *pollinasa*) and economic profits (Fig. 3). Only in SJ farm, increasing external feed (*pollinasa*) improved the economic results (Fig. 3). In the former studies of Flores-Sanchez et al. (2015) and Cortez-Arriola et al (2016), an important additional objective was to improve organic matter balance, which we did not consider although it could have improved the insights of long-term sustainability of alternative managements. Moreover, modelling alternative crops species and different management strategies and potential forest productive uses are issues that deserve to be more explored in future studies.

4.5 Practical implication and recommendations

Producing food in areas of great importance for biodiversity conservation is an issue that has recently gained much attention from world society. However, many inhabitants of these places face economic pressures and lack of support to be able to produce without falling into simplified extensive crops (Meyfroidt et al., 2014). As we show, there are no general land-use configurations and managements to be implemented in all TFS since each farm characteristic determines the multi-objective optimization and outcomes. Therefore, the analysis of particular cases, at least, at *ejido* level (as done in this study) is necessary to improve the agricultural production and forest conservation through sustainable practices. For farms with high potential to improve (i.e. QU, RA and ZPO), reconfiguring land-uses following alternatives of sustainable intensification could be the straightest pathway to improving agricultural production and forest conservation. For farms with less potential (SJ and LV), increasing external inputs appears as the straightest solution. However, incorporating new alternative land-uses (new crops and animal species) and a multi-objective optimization re-analysis could increase the potential to improve agricultural production and conservation.

5 Conclusions

We conclude that there is potential in TFS to simultaneously conserve the forest and increase agricultural production. However, improving these objectives through sustainable intensification practises was not feasible for all farms. Instead, the initial farm configurations determined the possibilities for satisfying all objectives. Considering that each initial farm configuration determined different alternative solutions which were not general for all farms, the

analysis of individual farms or at least, typical farms from typology groups emerges as a paramount aspect. Therefore, it is very important to not make generalization where these alternative strategies could determine different pathways for conservation and production.

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4.1 Capítulo 4: Figuras suplementarias

Strategies to overcome the conservation-production dichotomy in agricultural systems immersed in highly-biodiverse tropical landscapes should be highly context-specific to be successful

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Supplementary material

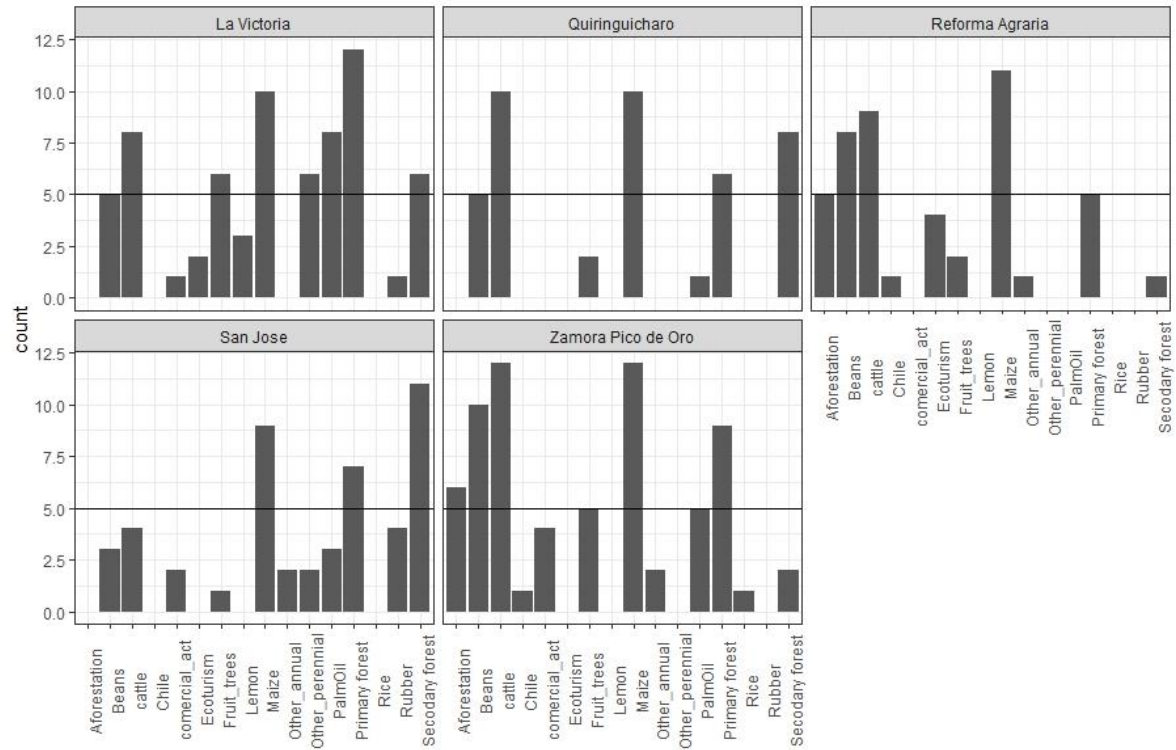


Figure 1: Land-uses counts in tropical farming systems (TFS) in five communities (grey tags) in Marqués de Comillas Region, Chiapas; México. The line set at $y=5$ indicates those activities considered to build the typical farms for each community.

Table 1: Selected land-uses for five typical tropical farming systems (TFS) in Marqués de Comillas region, Chiapas, México. Areas (ha) and calculation are specified.

Land uses	Community					Calculation
	La Victoria	Reforma agraria	Quiringuicharo	San Jose	Zamora Pico de Oro	
Fruit trees	1				1.5	Mode
Forest	16	20	13	9	14.5	Average
Maize-grain	1	2.65	0.58	2	3	Mode
Maize silage		1.35	2.41			Mode
Beans	1	1	0.77		1	Mode
Palm	24.5				11	Mode
Lemon	2					Mode
Cattle						
Fattening	16			13		Mode
Cattle calf breeding						Mode
Cattle mixed		18.5	53		48.5	Mode
Afforestation (Mohamy)					2	Mode
Farm area	61.5	43.5	69.76	24	81.5	Sum

Table 2: Inputs, outputs and management decisions for land-uses in five typical tropical farming systems in Maqués de Comillas region, Chiapas, México.

Activity	Variable	Units	Community				
			La Victoria	San Jose	Quiringuicharo	Reforma agraria	Zamora Pico de Oro
Beans crop	Grain yield	kg ha ⁻¹	1000		1000	1500	1733
	Labour	h ha ⁻¹ yr ⁻¹					
Maize crop	Labour	¹	595.4		595.4	595.4	595.4
	Grain yield	kg ha ⁻¹	3258	4298*	2443	5102	4441
	Fertilizer (Trile 17)	kg ha ⁻¹	75	150		200	93
	Fertilizer (18-46-0)					150	
	Fertilizer (Urea)	kg ha ⁻¹	154	200			112
	Herbicides (Glyphosate)	l ha ⁻¹	2.25			1.914	2.833
	Herbicides (Paraquat)	l ha ⁻¹	1.85	2		0.107	
	Insecticides (Chlorpyrifos)	l ha ⁻¹	1.6				
	Insecticides (Cypermethrin)	l ha ⁻¹	0.75	0.62		0.256	0.755
	Insecticides (Lufenuron)	l ha ⁻²				0.175	
Lemon	Labour	h ha ⁻¹ yr ⁻¹					
	Labour	¹	658	904*	1157	66.05	388.42
	Fruit yield	kg ha ⁻¹	18000				
	Labour	h ha ⁻¹ yr ⁻¹					
	Labour	¹	160				
Palm Oil	Fertilizer (Urea)	kg ha ⁻¹	100				
	Insecticides (chlorpyrifos)	l ha ⁻¹	1.5				
	Fruit yield	kg ha ⁻¹	23113				23800
	Fertilizer (Trile 17)	kg ha ⁻¹	335				104
	Herbicides (Glyphosate)	l ha ⁻¹	2.9				2.166
	Herbicides (Paraquat)	l ha ⁻¹	2.6				
Labour	Labour	h ha ⁻¹ yr ⁻¹					
	Labour	¹	300				300

Afforestation								
Mahogany	Biomass yield	kg ha ⁻¹						10000
		h ha ⁻¹ yr ⁻¹						
	Labour							595.4
Steers								
fattening	Number of steers	number	20	22				
	Replacement rate	steer yr ⁻¹	1.16	1.33				
	Grazing period	days	365	365				
		h ha ⁻¹ yr ⁻¹						
	Labour		179.5	179.5				
	Maize grain feed	kg yr ⁻¹	9500					
		kg MS						
	Grass feed	ha ⁻¹ yr ⁻¹	115984.4	60000				
	Pollinasa feed	kg yr ⁻¹	14000	14908.88				
Cattle mixed	Number of bulls	number			2	1	1	
	Number of cows	number			42	23	37	
	Number of calves	number			24	8	44	
	Number of steers	number			20	11	44	
	Replacement rate (steers)	steer yr ⁻¹			1.12	0.75	0.51	
	Grazing period	days			365	365	365	
		h ha ⁻¹ yr ⁻¹						
	Labour				594**	594**	594**	
	Grass feed	kg MS ha ⁻¹ yr ⁻¹			252454	43012.5	157625	
	Maize grain	kg yr ⁻¹				4336		
	Maize silage	kg yr ⁻¹			9957.2	50000		
	Pollinasa feed	kg yr ⁻¹						306750.9

* Two maize seasons (tornamil and tapochol) are summed in grain yield and labour values, ** Labours incurred in bulls, cows, calves and steers are summed.

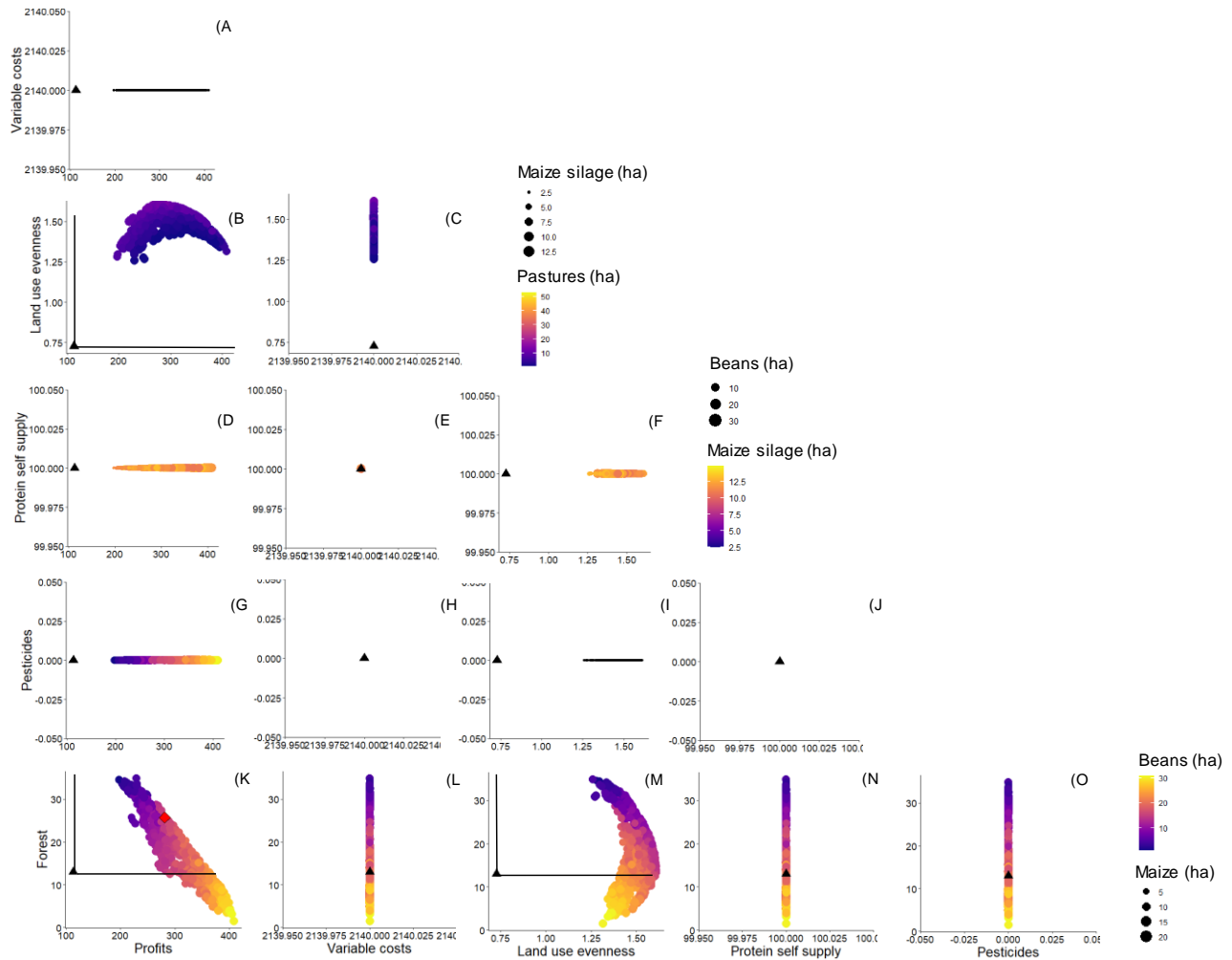


Figure 2: Relations between optimization objectives for Quiringuicharo farm. Each dot represents one alternative solution which that satisfies the optimizations. Triangles, farm current situation; 90 degrees black lines represent synergies that improve the current situation. For those objectives in Y-axis the two most correlated farm drivers (variables) are detailed with colours (first correlated) and dot size (second correlated).

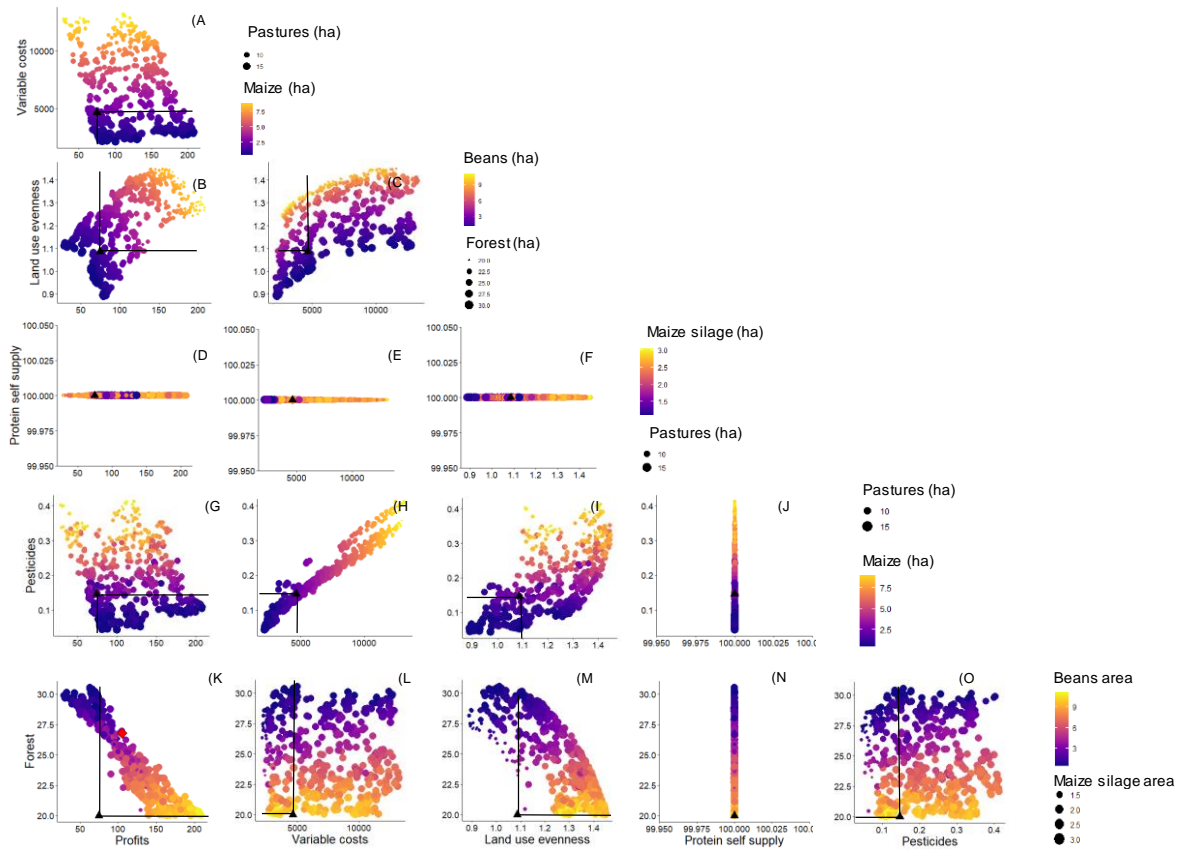


Figure 3: Relations between optimization objectives for Reforma Agraria farm. Each dot represents one alternative solution which that satisfies the optimizations. Triangles, farm current situation; 90 degrees black lines represent synergies that improve the current situation. For those objectives in Y-axis the two most correlated farm drivers (variables) are detailed with colours (first correlated) and dot size (second correlated).

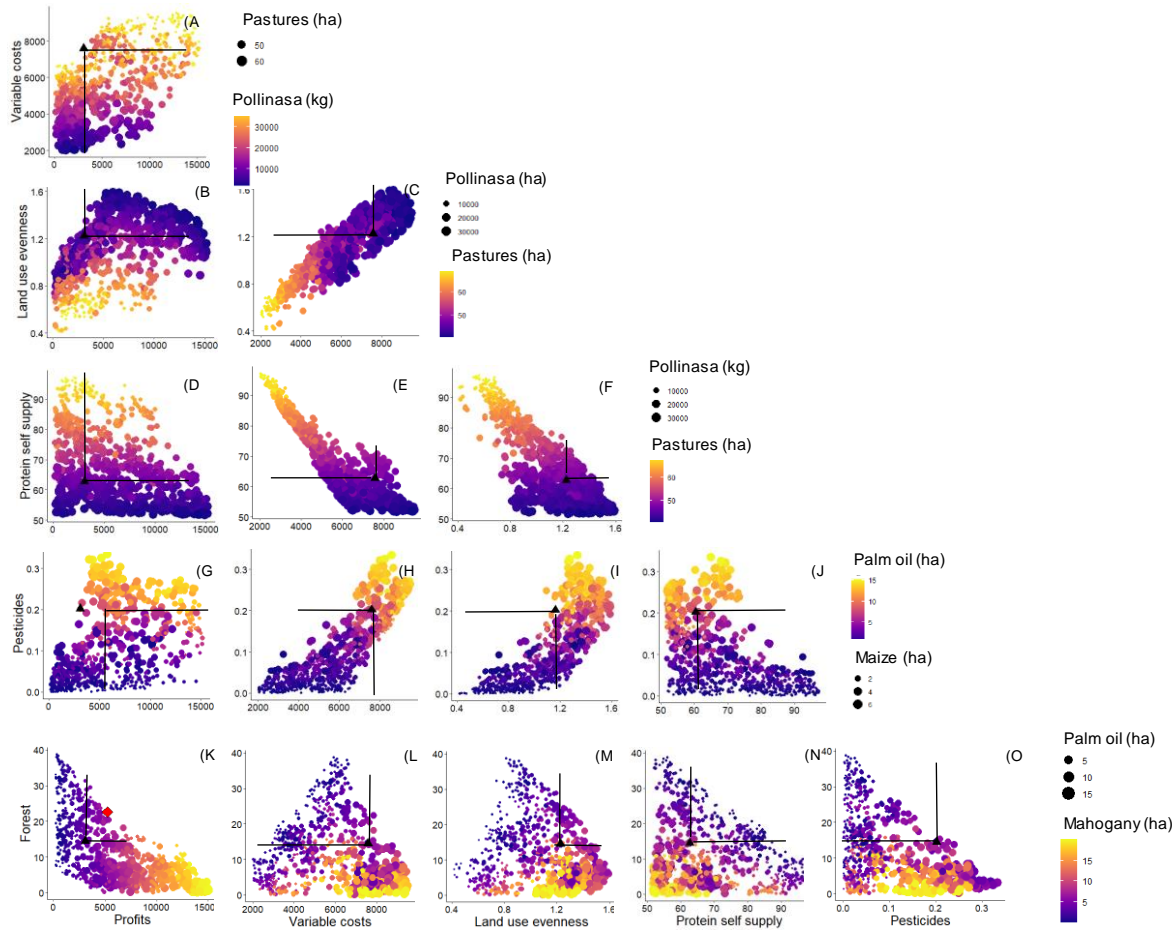


Figure 4: Relations between optimization objectives for Zamora Pico de Oro farm. Each dot represents one alternative solution which that satisfies the optimizations. Triangles, farm current situation; 90 degrees black lines represent synergies that improve the current situation. For those objectives in Y-axis the two most correlated farm drivers (variables) are detailed with colours (first correlated) and dot size (second correlated).

Capítulo 5: Discusión general y conclusiones

5.1 Discusión general

El objetivo general del proyecto de tesis fue investigar qué composición y configuración de PMH promueven balances positivos entre los componentes de conservación y de producción agropecuaria. Los resultados del capítulo uno, relacionado con el componente de conservación de la biodiversidad y de las funciones y servicios ecosistémicos a la escala de paisaje revelan, en primer lugar, que el efecto de los cambios en la configuración del paisaje (i.e., distribución, tamaño y forma de los fragmentos de selva remanentes en el paisaje) sobre este componente es casi despreciable comparado con los efectos producidos por cambios en la composición del paisaje (i.e., cantidad de hábitat de selva remanente en el paisaje) a medida que avanza el proceso de conversión de selvas a campos agropecuarios. Específicamente, se encontró que al menos el 40% del área de los PMH deberían permanecer sin deforestarse para mantener niveles de diversidad de especies de árboles comparables a aquellos paisajes completamente cubiertos.

Este resultado parece prometedor y pragmático. Sin embargo, cuando se observó la función y servicio ecosistémico relacionados con la producción de biomasa y el almacén de C, los efectos de la deforestación fueron diferentes. A diferencia de la trayectoria de poco cambio de la diversidad con la deforestación hasta alcanzar un umbral sobre el cual la diversidad se colapsa, ambos atributos disminuyeron exponencialmente desde que se inicia el proceso de deforestación. Este resultado muestra que la trayectoria de cambio de la biodiversidad con el aumento de la deforestación en el paisaje no es indicativa de lo que puede suceder con otros atributos del ecosistema en respuesta a la deforestación. Los umbrales críticos en la diversidad de especies y la documentación de estas respuestas diferenciales del ecosistema de selva a la deforestación son los descubrimientos más importantes en este capítulo. Futuras investigaciones relacionadas con

el análisis de trayectorias de cambio en la diversidad de otros organismos y de otras múltiples funciones y servicios ecosistémicos con el avance de la deforestación, diferentes a las aquí estudiadas, aparecen como un desafío clave para comprender más profundamente cuánto y cómo conservar en los PMH.

Posteriormente se analizó cómo factores biofísicos, socioeconómicos y culturales y agronómicos determinan, a través de las decisiones de manejo, el tipo de sistema de cultivo de maíz, su rendimiento y sustentabilidad. Los resultados del capítulo dos mostraron que, en la región de estudio, los sistemas de cultivo preponderantes fueron los convencionales (CS) y tradicionales (TS). El tipo de suelo (componente biofísico) fue un factor determinante a la hora de tomar decisiones sobre la cantidad de fertilizante a aplicar (componente agronómico) y además sobre la variabilidad del rendimiento, independientemente del tipo de sistema de cultivo. Más aún, se esperaba que los insumos agronómicos industriales (fertilizantes y pesticidas) tuvieran un impacto positivo en el rendimiento de grano. Por el contrario, no se encontraron respuestas positivas de estos insumos sobre el rendimiento en ningún sistema de cultivo.

Llamativamente, en los TS se encontraron correlaciones negativas entre la aplicación de glifosato y el rendimiento de maíz (por posibles efectos de fitotoxicidad). Los resultados encontrados proveen evidencias de que existe un manejo agronómico inconsistente en los sistemas de cultivo de maíz, donde los insumos no se traducen en un mayor rendimiento, amenazando así la sostenibilidad de los sistemas agrícolas. Este resultado muestra un ejemplo de las potenciales externalidades que la simplificación de los sistemas agropecuarios puede estar produciendo en las parcelas agrícolas inmersos en la dinámica de los PMH.

Por último, se analizaron balances potenciales entre la conservación y la producción a escala de sistemas de producción agropecuarios (TFS). En general hubo una fuerte disyuntiva (trade-off) entre aumentar las áreas de conservación y aumentar los beneficios económicos a través del aumento de la producción. La configuración y el manejo agropecuario realizados en cada TFS determinaron la capacidad de balancear ambos componentes. Aquellos TFS que ya se encontraban muy intensificados (alta carga de animales e insumos externos) tienen bajo potencial para incrementar áreas de bosque e ingresos económicos. Aun así, los resultados muestran que una manera de lograrlo es a través de incrementar costos variables asociados al aumento en insumos externos, es decir, dejando a un lado criterios de intensificación sustentable. Por el otro lado, en los TFS con mayor potencial para un aumento en las áreas de bosque y de ingresos económicos, lograrían este objetivo a través de incrementar el número de cultivos con mayor rentabilidad (frijoles, forestaciones de Cedro, *Cedrela Odorata*, y Caoba, *Swietenia macrophylla*) e incrementar áreas para auto-provisión de alimento para el ganado (maíz en grano o silaje). Este procedimiento aumentaría la diversificación y la resiliencia (bajando dependencia de insumos externos) de los cultivos y disminuiría los costos variables, llevando a establecer pautas para una intensificación de la producción que sea sustentable y compatible con la conservación.

Para una región donde se podría considerar que los recursos abióticos (suelo, precipitaciones, radiación) son homogéneos, el componente socioeconómico-cultural (cantidad de tierra disponible, nivel de insumos, preferencias en el manejo, etc.) determinó el tipo de configuración inicial de los TFS. Estas características iniciales determinaron respuestas diferenciales a la optimización multi-objetivo y en consecuencia a sus capacidades de balancear la conservación y

la producción. La exploración de alternativas para resolver la dicotomía entre “conservar y producir” generó soluciones concretas para balancear estos componentes, incluso, incrementarlos. Por último, la interrelación y acuerdos entre todos los actores interesados, incluyendo a los tomadores de decisiones en los TFS, a los tomadores de decisiones ejidales y a todas las instituciones involucradas/interesadas dentro de los PMH, ayudaría a integrar este rediseño de los TFS y en consecuencia mejorar los balances entre conservación y producción a escala de PMH.

5.2 Límites y bondades de las aproximaciones experimentales de la tesis

5.2.1 Limitación en el objetivo 1

Está claro que, al abordar preguntas de investigación relacionadas a temáticas ecológicas, productivas y sociales en los PMH, el desafío de la definición de límites y escalas surgió rápidamente. Para desarrollar el primer objetivo, las disciplinas y el marco teórico que dieron sustento a la pregunta fueron la “ecología espacial y del paisaje”. Para este tipo de preguntas la ecología del paisaje considera dos aproximaciones generales de diseño experimental, uno es el diseño de parche-focal (o parche-paisaje) y el otro es el diseño a escala de paisaje (el utilizado en este estudio, Fletcher y Fortin, 2018). En el primero las variables respuesta se miden en el “parche focal” y las explicativas en el paisaje circundante a diferentes tamaños asumiendo que las respuestas encontradas en el muestreo central son atribuibles a la variación estructural circundante (Fig. 5.1, izquierda). En el segundo, se describe la estructura total de las unidades de paisaje y se la considera como variable explicativa y también se obtienen muestras de las variables respuesta en toda la unidad (Fig. 5.1, derecha, Zonneveld, 1989).

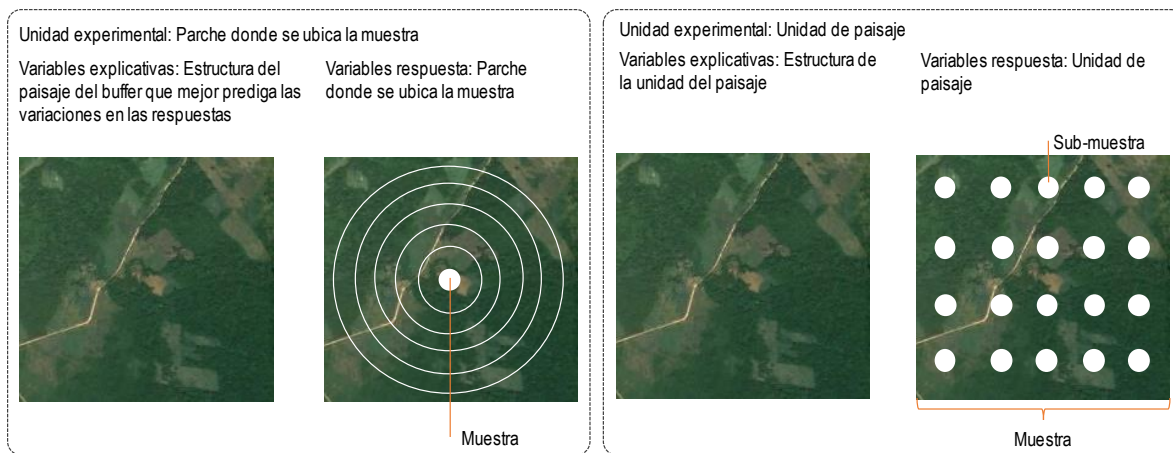


Figura 5.1: Aproximaciones experimentales de la ecología del paisaje. Izquierda, diseño de “parche-focal” que asocia las variables respuestas a estructuras del paisaje de un tamaño que mejor prediga los modelos asociados. Derecha diseño a “escala de paisaje” donde tanto la estructura del paisaje como las variables respuestas son medidas en la unidad de paisaje. Círculos concéntricos indican las parcelas focales que potencialmente se asociarían con las variables respuesta.

Las ventajas del diseño parche-focal son: i) un rápido muestreo de la unidad experimental (se muestrea el parche), ii) esto permite incrementar el número de muestras (N), iii) con el aumento de N, aumentan los grados de libertad en los modelos, iv) esto permite probar modelos con mayor cantidad de parámetros y así lograr mayor predictibilidad. Algunas desventajas son, que se asume que el valor de las respuestas es debido a la estructura de paisaje circundante. Este supuesto puede debilitarse si, el ambiente circundante tiene factores no identificados. Por ejemplo, si en el parche se estuviesen midiendo cantidad de propágulos que llegan por dispersión y en el buffer hay un accidente geográfico (una gran barranca) se podría inferir que no hay propágulos por la estructura de paisaje y en realidad es por la diferencia topográfica. Lo mismo ocurriría si el paisaje está dividido por una ruta o río, esto podría causar inaccesibilidad hacia el parche. En definitiva, al no muestrear los buffers completos, puede existir incertidumbre acerca

de los efectos reales del alrededor sobre el parche (Jackson y Fahrig, 2015). Esta aproximación es muy utilizada para especies móviles como mamíferos terrestres y aves (Carrara et al., 2015; Galán-Acedo et al., 2018; Garmendia et al., 2013)

La principal ventaja del diseño a escala de paisaje es que se obtiene una representación completa tanto de las variables explicativas (estructura del paisaje) como de las respuestas (sub-muestras describen al paisaje completo, Fig. 5.1 derecha). Esto permite absorber las variaciones intra-paisaje que podrían sesgar las respuestas. Por ejemplo, si en el paisaje hay un río o una ruta, se muestrearán ambos lados, pudiendo así absorber posibles efectos en el error experimental. La desventaja mayor es que el esfuerzo de muestreo es enorme. Entonces, en general, las unidades de paisaje son escasas (bajo N) y esto acarrea que se dispongan pocos grados de libertad y difícilmente se puedan probar modelos con más de dos o tres parámetros (Jackson y Fahrig, 2015). A pesar del enorme esfuerzo de muestreo se optó por este último tipo de experimento. Al obtener un tamaño de muestra de $N=20$ se logró aplicar regresiones lineales segmentadas para encontrar puntos de inflexión en la trayectoria de las respuestas y también fue posible ajustar ecuaciones asintóticas de dos parámetros como la de Michaelis-Menten.

5.2.2 Limitaciones y bondades en el objetivo 2

Para responder la segunda pregunta de investigación, se hizo necesario reducir la escala y dejar al paisaje de lado ya que, el lote/parcela, es la unidad menor, dentro de los PMH, donde, son aplicadas las decisiones de los agricultores. Tal como se mencionó en la introducción, existen múltiples actividades dentro de los PMH. La ganadería extensiva, el cultivo de palma de aceite y de maíz son los preponderantes en la región de estudio. Dentro de éstas, la ganadería es la que

mayor área abarca y luego, si está presente, la palma de aceite (ver información suplementaria, Cap. 4). Sin embargo, se eligió poner foco en los sistemas de cultivo de maíz porque: i) fue el uso más frecuente en toda la muestra de TFS (51 sistemas de cultivos de maíz en 63 TFS analizados), ii) porque estos sistemas son los que más diversidad de insumos agrícolas demandan (herbicidas, insecticidas, fertilizantes, semillas, maquinaria y/o horas de labor) y, por último, iii) al utilizar tantos insumos y formas de manejo existía una mayor variación en la toma de decisiones que podrían enriquecer el análisis, no solo a escala de sistema de cultivo, sino en niveles superiores. Tal ejemplo fue cómo los tipos de sistemas de maíz se agruparon en aquellos donde los agricultores compartían similares sitios de origen, asociándose luego, a los distintos ejidos (Cap. 3).

Para una mayor comprensión de cómo los factores estudiados impactan en el rendimiento global de los sistemas y en los PMH sería necesario replicar éste análisis a los sistemas de producción ganadera (cría, engorde y mixtos), los de palma africana de aceite y de hule (brevemente descritos en información suplementaria del Cap. 4). Estos estudios adicionales darían una visión más completa al incluir actividades que abarcan mayor superficie dentro de los PMH y además generan mayores ingresos de divisas en la economía de los campesinos.

En relación al componente socioeconómico y cultural estudiado en este capítulo, se consideró aquellas variables que presumiblemente tuvieran un efecto directo sobre los sistemas de cultivo de maíz (e.g. tamaño total del sistema de producción, edad, otorgamiento de planes de promoción de la producción, etc.). Sin embargo, la interacción con las y los agricultores en las entrevistas dejó de manifiesto que existen relaciones más complejas entre las personas y el

sistema de estudio. Los agricultores manifestaron informalmente algunos factores que no entraron en el modelo de análisis. Las asimetrías de poder con los comerciantes compradores de productos (denominados coloquialmente “coyotes”), la imposibilidad de crear o elegir otra vía de comercialización por eventuales sucesos de inseguridad y la gran distancia hacia los grandes centros urbanos son algunas limitaciones mencionadas y que muy presumiblemente estén influenciado al sistema de estudio (algunos de estos factores han sido mencionados en Galvan-Miyoshi et al., 2015). Por otro lado, del total de la muestra (N=51) hubo solo cuatro mujeres entrevistadas. El desbalance no permitió incluir al género como variable de estudio, sin embargo, estas cuatro agricultoras mostraron sistemas de maíz tradicionales con baja carga de pesticidas y alta carga de trabajo manual independientemente el ejido donde se encontraban. Las relaciones de género y el tipo de manejo de plantas ha sido bien documentadas en otras eco-regiones de México (Lira et al., 2016). Futuras investigaciones de los factores sociales subyacentes que modulan los sistemas de producción a través de aproximaciones cualitativas serían muy pertinentes para una mejor comprensión de las relaciones de las y los agricultores y estos PMH.

Por último, es importante en éste inciso resaltar algunas debilidades en la toma de datos que surgieron durante el desarrollo de éste capítulo que merecen ser expuestas y explicadas a fin de reconocer y tomar recaudos sobre las conclusiones obtenidas en el capítulo 3. Tanto las variables explicativas (fertilizantes, herbicidas, insecticidas, litros de diésel y horas de labor) como la principal variables respuesta (rendimiento) en los sistemas de cultivo de maíz fueron tomadas a través de entrevistas. A los agricultores se les preguntó cuál es el rendimiento típico correspondiente al manejo característico que se realiza en cada TFS. Esta pregunta incurre que el entrevistado podría proveer un valor no exacto o vago. Trabajos similares hechos con entrevistas

a campo, en general, preguntaron sobre el rendimiento de la campaña anterior (Mascorro-de Loera et al., 2019). Desde mi perspectiva existen debilidades en ambas maneras de preguntar. En el caso de preguntar sobre la campaña anterior, los valores serían más exactos, pero traerían absorbida la interacción entre las variables preguntadas y el ambiente que experimentó el cultivo. Por ejemplo, la fertilización tiene mayores efectos sobre rendimiento en años con lluvias apropiadas comparada con años de lluvias escasas. En cambio, cuando la pregunta es sobre valores típicos, el entrevistador asume y confía en la percepción del agricultor acerca los resultados obtenidos para las prácticas típicas descritas. La debilidad en esta aproximación radica en que el valor carece de precisión, sin embargo, de alguna manera deja de lado las posibles anomalías ambientales que el valor de una sola campaña podría acarrear.

5.2.3 Límites y bondades en el objetivo 3

La modelación de sistemas multi-objetivo a escala de sistemas de producción agropecuarios es una herramienta que está ganando gran atención en la comunidad científica-agronómica. Esto se debe a que la multiplicidad de resultados originados a través de la optimización de Pareto permite encontrar opciones alternativas de manejo que en las situaciones actuales no eran pensadas o ejercitadas (Groot et al., 2012). Estas opciones alternativas pueden ser fuente de inspiración para discusiones de cómo lidiar con componentes aparentemente opuestos (por ejemplo, conservación *vs.* producción) en reuniones participativas entre académicos y campesinos.

Al hablar de escalas, queda, sin embargo, el interrogante de que si sería posible modelar todo el conjunto de sistemas de producción incluidos en una unidad de paisaje (o en todas). La respuesta rápida es que sí. Existen ejemplos a escalas superiores (mosaicos de cultivos y paisajes) de modelación de sistemas multi-objetivo donde se ha modelado los beneficios económicos, la calidad del paisaje y conservación en paisajes en el norte de los Países Bajos, como también se ha modelado potenciales disyuntivas (trade-offs) entre servicios ecosistémicos en paisajes de África, Latinoamérica, Asia y Europa (Chopin et al., 2015; Groot et al., 2007, 2018).

5.2.4 Las escalas del proyecto

Para lograr una comprensión integral del espacio y escalas donde las preguntas de investigación se respondieron, en la figura 5.2 se describen los niveles de organización biológica, los cuales son utilizados como marco de estudio en la biología y en la ecología del paisaje (de lo singular a lo complejo son: individuos, poblaciones, parches/comunidades, paisajes, ecosistemas y biomas) y los niveles de organización socio-políticos-productivos, que son el resultado de la geografía política de un país más las organizaciones comunes que un tomador de decisiones puede ejercer en el terrero para organizar el sistema de producción agropecuario (de lo singular a lo complejo son: plantas/animales, lote/potrero, sistemas de producción agropecuarios, ejidos, municipios y estados; Fig. 5.2). Ambas aproximaciones tienen paralelismos que permiten su interrelación. Mientras que el objetivo 1 de la presente tesis se respondió a escala del paisaje, determinándose éstos de manera arbitraria para lograr el gradiente de deforestación, el objetivo 2 se respondió a escala de lote, la mínima unidad, donde un agricultor toma decisiones de manejo. Por último, el

objetivo 3 se respondió a escala de sistema de producción donde múltiples actividades agropecuarias son llevadas a cabo y también existen parches de selva para la conservación.

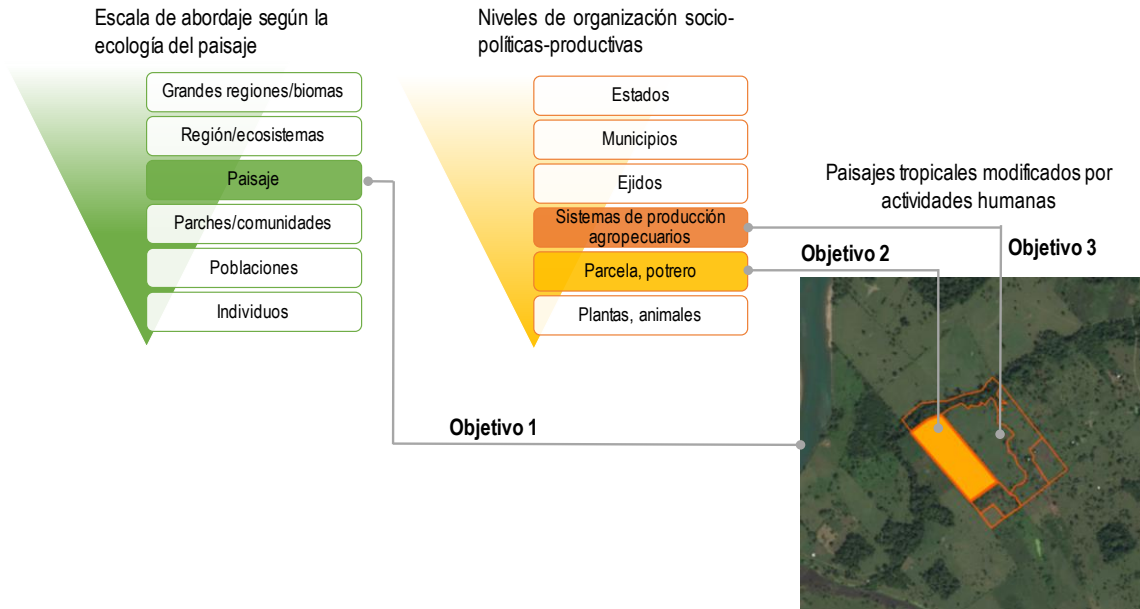


Figura 5.2: Niveles de organización o escalas de abordaje en la ecología del paisaje (izquierda) y niveles de organización socio-políticas-productivas (derecha). El objetivo 1 se respondió a escala de paisaje (imagen completa), el objetivo 2 a escala de lote (cuadrado amarillo) y el objetivo 3 a escala de sistema de producción (líneas naranjas).

5.2.4 Aportes al modelo “Land sharing vs. Land sparing”

El ingeniero agrónomo Norman Borlaug, descubrió el trigo enano a fin de la década de 1950 dando comienzo a la revolución verde (Borlaug, 2007b). Junto a este movimiento, surgió la hipótesis de que el incremento en los rendimientos por hectárea de los cultivos a través de fitomejoramiento, manejo de cultivos, labranzas, fertilización, control de malezas y plagas y manejo del agua podría no solo “combatir el hambre mundial” sino que también liberar tierras para la

conservación (Borlaug, 2007a). Ésta hipótesis se sustenta en que la intensificación agrícola, al aumentar los rendimientos por hectárea, produce un aumento en la oferta de productos alimenticios que deprime los precios e induce a los agricultores a abandonar tierras o abstenerse de cultivar (Rudel et al., 2009). Por otro lado, en ecología de la conservación se postula el modelo *land sharing* (“*tierra compartida*”, sistemas agrícolas con bajos rendimientos y con bajos impactos ambientales) vs. *land sparing* (“*ahorro de tierra*”, sistemas intensificados con altos rendimientos y con baja demanda de tierras, siguiendo la hipótesis de N. Borlaug). El primero se caracteriza por una agricultura de bajos insumos y rendimientos y practicas amigables con la naturaleza y el segundo se describe como agricultura intensiva de altos rendimientos con baja demanda de tierras (Kremen, 2015).

Siguiendo este argumento lógico para el caso de estudio de la presente tesis, se podría esperar que los sistemas de producción con mayor uso de insumos, mayor producción y mayor beneficio económico presenten mayor proporción de áreas de bosque, según la premisa de *Land sparing*. Para describir los ingresos y producción de los TFS, en la figura 5.3 se muestra la relación entre la superficie total y los beneficios económicos totales en el año para los cinco sistemas de producción analizados. El gradiente de colores y de tamaños de puntos muestran el nivel de agroquímicos y la densidad de animales como indicadores de intensificación productiva. Claramente, no existe una relación directa (lineal positiva) entre el tamaño del TFS y el beneficio económico obtenido. Más bien, aquellos sistemas que incluyen dentro de los usos a la palma aceitera mostraron mayores ingresos económicos independientemente el tamaño del TFS (ejidos LV y ZPO, La Victoria y Zamora Pico de Oro, respectivamente).

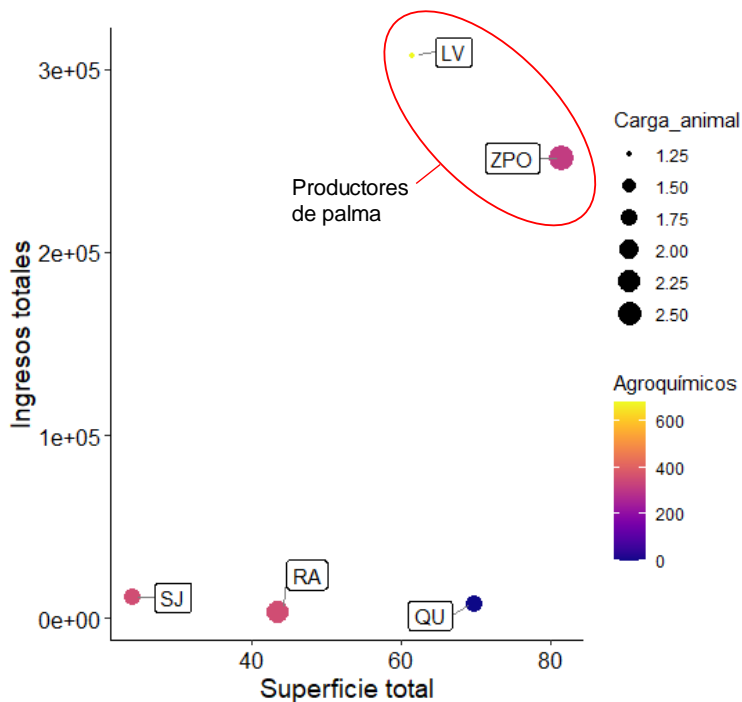


Figure 5.3. Relación entre ingresos económicos totales en un año (US\$ año⁻¹) y la superficie total de los sistemas de producción agropecuarios (TFS en ha). Escala de colores indica el nivel de uso de agroquímicos (kg ha año⁻¹) y el tamaño de los puntos la carga animal (animales. ha⁻¹). Cada punto indica un TFS modal de cada ejido (LV, La Victoria; SJ, San José; QU, Quiringuicharo; RA, Reforma Agraria y ZPO, Zamora Pico de Oro).

Al analizar el nivel de intensificación por hectárea (aquí es muy importante remarcar que la intensificación puede ser industrial, con aumento de uso de insumos, o ecológica, utilizando prácticas de intensificación sustentable, descritas en el capítulo 4), se podría esperar que aquellos TFS con mayor uso de insumos industriales tengan mayor producción e ingresos por hectárea y, en consecuencia, mayor proporción de área para la conservación. En LV y ZPO, se obtuvieron los mayores ingresos por hectárea con los mayores niveles de insumos (asociados a la palma,

Fig. 5.4 A), pero la proporción de selva conservada en estos ejidos es menor comparada con los TFS con bajo nivel de intensificación (Fig. 5.4 B). Por otro lado, existió un uso intermedio de agroquímicos con un amplio rango de ingresos económicos (ver para, RA, SJ y ZPO en Fig 5.4 A) y porcentajes de conservación (ver para, RA, SJ y ZPO en Fig. 5,4 C). De estos tres últimos, llamativamente los TFS con menor beneficios económicos por hectárea y menor superficie total, es decir SJ y RA, fueron los TFS con mayor proporción de selva en conservación dentro de la superficie total del sistema (Fig 5.4 B). Es decir, la proporción de selva para la conservación no estuvo determinada por mayores ingresos, ni por mayor superficie total de TFS.

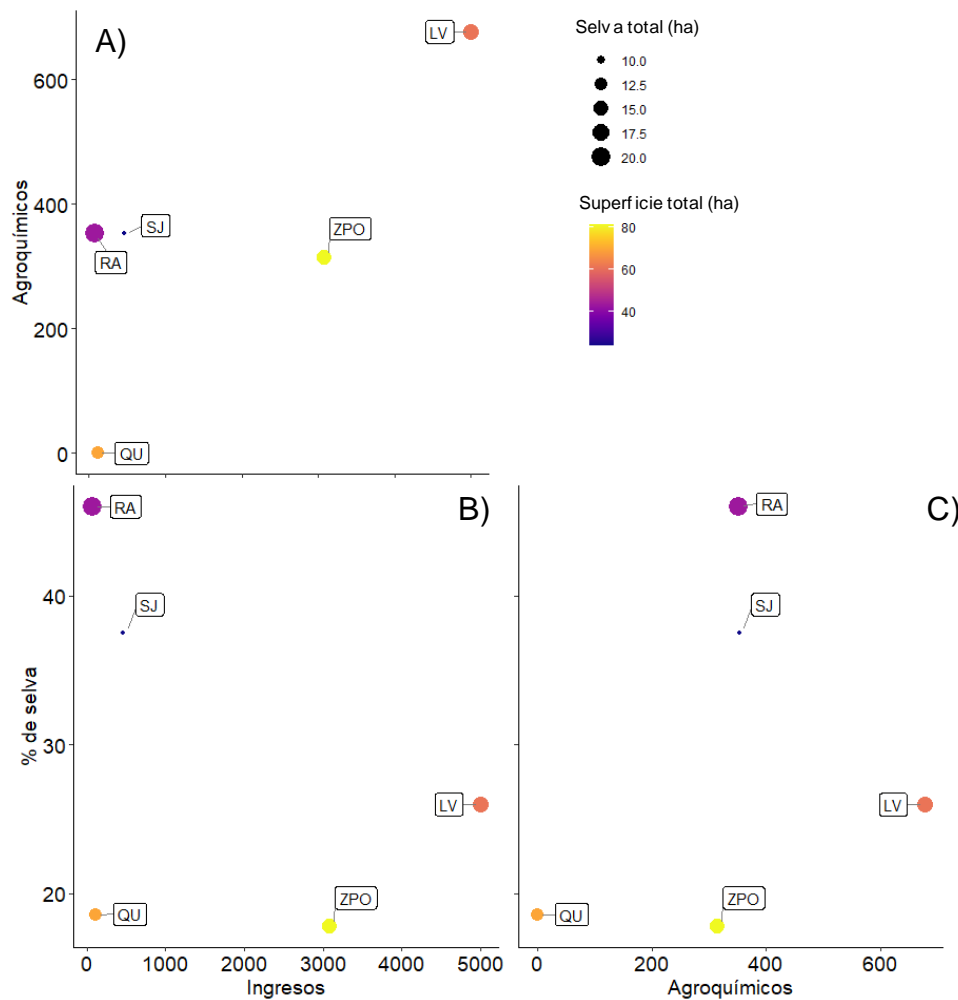


Figure 5.4: Exploración de relaciones entre componentes de conservación y producción en sistemas de producción agropecuaria (TFS) en Marqués de Comillas, Chiapas. A) Relación entre beneficios económicos, usos de agroquímicos por hectárea y porcentaje de selva en el TFS, B) relación entre el porcentaje de selva en conservación y los beneficios económicos por hectárea, C) relación entre el porcentaje de selva en conservación y los usos de agroquímicos por hectárea. Escala de colores indica el total de la superficie del TFS (ha) y el tamaño de los puntos el área total de selva conservada (ha). Cada punto indica un TFS modal de cada ejido (LV, La Victoria; SJ, San José; QU, Quiringuicharo; RA, Reforma Agraria y ZPO, Zamora Pico de Oro).

Los TFS de este estudio proveen ejemplos de que la estrategia de aumentar la productividad por hectárea a través de incrementar insumos para liberar proporciones de área para la conservación no sería efectiva. Contrariamente, aquellos TFS con menores beneficios económicos de la producción fueron los que mayor proporción de selva mantuvieron (RA y SJ). Se ha mostrado que la estrategia *land sparing* podría tener efectividad en países “desarrollados” donde el sector agropecuario es altamente subsidiado y los estándares económicos de los productores no son amenazados. Sin embargo, en los países en desarrollo, donde los sistemas de producción tienen altas cargas impositivas y bajos subsidios, el incremento de los rendimientos producirían más beneficios económicos pero aunado a mayor deforestación y menor proporción de conservación dentro del TFS, es decir tendrían el efecto contrario (Ewers et al., 2009).

La necesidad de encontrar sistemas de producción sustentables, en armonía con la naturaleza, parece haber encontrado su contracara que es el creciente aumento de la población mundial y por consiguiente el aumento de la demanda de alimentos, fibras y energía a cualquier costo (social, ambiental, incluso económico). Ester Boserup planteó el concepto de intensificación agrícola en su libro “The Conditions of Agricultural Growth” en 1965, como respuesta a la teoría de Malthus

que predecía hambrunas en el futuro a causa del crecimiento exponencial de la población mundial (Malthus, 1798). Hoy día se sabe que la intensificación agrícola no es una. Si sólo se considera a la intensificación basada en insumos para incrementar los rendimientos por hectárea, queda en entredicho, por lo menos para estos casos de estudio que ni la sustentabilidad de los sistemas ni la conservación pueden alcanzarse. Por otro lado, la intensificación ecológica (o sustentable como se abordó en el capítulo 4) se define como el medio para hacer uso intensivo e inteligente de las funcionalidades naturales del ecosistema (soporte, regulación) para producir alimentos, fibra, energía y servicios ecosistémicos de forma sostenible (Tittonell, 2014). La principal diferencia entre ésta y la intensificación industrial está en el rol que cumple la naturaleza en la dinámica de los TFS y en las posibles sinergias entre la producción de alimentos y el equilibrio dinámico de ésta con la biodiversidad y las funciones y servicios que esta provee (Doré et al., 2011; Tittonell, 2014).

5.3 Conclusiones

Los balances entre la conservación de selvas húmedas y la producción de alimentos para la auto-suficiencia y las sociedades son posibles. A continuación, se enumeran las conclusiones que sustentan esta idea inicial de la tesis.

En relación al capítulo 1.

- Mantener en el paisaje más del 40% de cobertura de selvas permitirían asegurar la presencia de una diversidad de especies arbóreas comparable a paisajes que se encuentran totalmente cubiertos por selvas.
- Aunque este porcentaje garantizaría una diversidad de especies de árboles significativa, no garantiza el correcto funcionamiento de funciones y servicios claves del ecosistema como son la producción de biomasa forestal y el almacenaje de C.
- Estos atributos ecológicos decrecen exponencialmente con el avance de la frontera agrícola. Esto evidencia una multiplicidad de respuestas en las trayectorias de estos atributos. Será imperativo el estudio de otros grupos de organismos y de múltiples atributos ecológicos en PMH en futuras investigaciones para desentrañar otras posibles trayectorias y definir, de manera integral, umbrales críticos de cobertura de selvas que ayudaría a conservar la biodiversidad, funciones y servicios del ecosistema de selva en estos paisajes.

En relación al capítulo 2

- Los sistemas de cultivo de maíz del sureste de México responden a factores biofísicos como la calidad de suelo. Estas variaciones intentan ser compensadas con decisiones de manejo agronómico como el agregado de fertilizante.

- Sin embargo, las herramientas aplicadas de manejo agronómicos no se traducen en mayores rendimientos. Existe inconsistencia entre las decisiones manejo de los cultivos en relación a los efectos que éstas tienen en los rendimientos reales.
- Existe un fuerte componente socio-cultural como el lugar de origen que determinó el tipo de sistema de cultivo de maíz.
- Considerando al componente socio-cultural, el codesarrollo de conocimiento participativo entre los agricultores, autoridades y académicos, es necesario para re-ajustar los sistemas de producción agrícola y lograr mayores eficiencias y eficacias de las decisiones de manejo sobre el rendimiento de los cultivos de maíz.

En relación al capítulo 3

- Es posible incrementar los beneficios económicos y las áreas de selva dentro de los TSF aunque éstos tengan diferentes configuraciones.
- Sin embargo, el potencial de optimización está fuertemente determinado por las condiciones iniciales de los TFS y cada TFS muestra diferentes caminos hacia la optimización.
- Entonces, no existen prácticas generales que mejorarían las disyuntivas entre la conservación y la producción en todos los TFS. Más bien, el aprendizaje proviene de asumir a cada TFS con su singularidad.
- La discusión e intercambio de la información obtenida en este estudio entre actores involucrados, junto con la retroalimentación por parte de los interesados

de la factibilidad de las recomendaciones para la mejora, es imprescindible para lograr el objetivo de encontrar un equilibrio entre la conservación y la producción.

5.3.1 Conclusiones generales

Los PMH necesitan de importantes porcentajes de selva para asegurar la permanencia y perpetuidad de especies y para que éstas sigan aportando múltiples funciones y servicios ecosistémicos. Las y los campesinos toman decisiones sobre sus sistemas de producción agropecuarios en íntima relación y en respuesta a factores biofísicos, socioculturales y agronómicos. Ésta decisiones determinan tanto el éxito del resultado productivo como también la generación de potenciales externalidades e incluso la necesidad de mantener o deforestar nuevas áreas para satisfacer nuevas necesidades productivas o económicas. El sistema de producción agropecuario, es la unidad fundamental donde las/los campesinos toman decisiones y éstas repercuten en el paisaje global. Cada ejido presenta características particulares, tanto para conservar como para producir.

Dada la singularidad de cada TFS, no existen decisiones de manejo únicas. La retroalimentación entre la experiencia singular de los involucrados (campesinas/os, autoridades ejidales, instituciones) con información como la generada en esta tesis permitirían pasar de un manejo separado a un manejo “integrado” (Fig 5.5). Así, las decisiones no sólo se focalizarían en la producción, sino también, en las posibles externalidades e impactos en el ambiente, en el manejo de la conservación en el sistema de producción y en el paisaje, ganando conciencia de los beneficios que estos proveen al bienestar común.

Este proyecto intentó explorar y generar información útil que permita idealmente acercarse un modelo de PMH integrados.

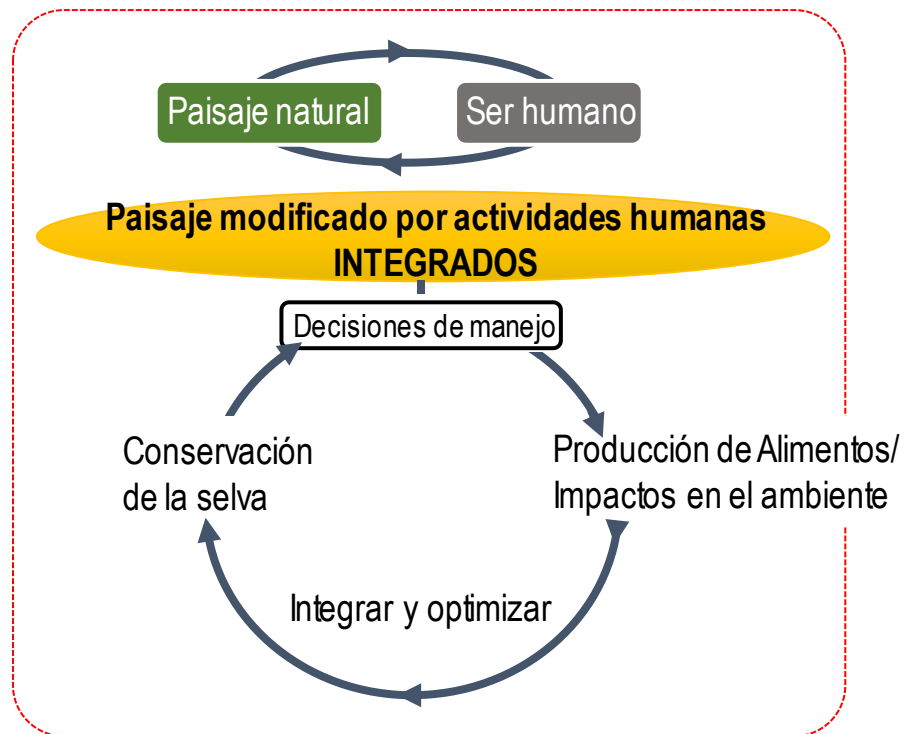


Figure 5.5: Marco conceptual de paisajes modificados por actividades humanas con una visión integradora. Las decisiones de manejo no tienen un solo propósito de producir alimentos, sino que consideran los impactos en el ambiente y las estrategias de conservación a escala de sistema de producción y de paisaje. Las flechas direccionales, como las presentadas en el marco conceptual de la introducción, cambian hacia flechas circulares. Esta circularidad intenta representar dicha integración de los componentes de conservación y producción en los pasajes modificados por actividades humanas.

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