



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD
ECOLOGÍA

DEMOGRAFÍA DE ESPECIES PIONERAS Y SUCESIÓN SECUNDARIA DE UN
BOSQUE TROPICAL HÚMEDO

TESIS

POR ARTÍCULO CIENTÍFICO

**DEMOGRAPHIC VARIATION AMONG PIONEER TREE SPECIES DURING OLD-
FIELD SUCCESSION OF A NEOTROPICAL RAINFOREST**

QUE PARA OPTAR POR EL GRADO DE:

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA:

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MORELIA, MICHOACÁN

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Me permito informar a usted que en la reunión ordinaria del Subcomité de Ecología y Manejo Integral de Ecosistemas, del Posgrado en Ciencias Biológicas, celebrada el día 30 de septiembre de 2019, se aprobó el siguiente jurado para la presentación del examen de grado de MAESTRA EN CIENCIAS BIOLÓGICAS en el campo de conocimiento de Ecología, de la estudiante GALLEGO MAHECHA MARÍA DEL MAR, con número de cuenta con 517024825, por la modalidad de graduación de tesis por artículo científico titulado: "Demographic differentiation among pioneer tree species during old-field succession of a Neotropical rainforest", que es producto del proyecto realizado en la maestría que lleva por título, DEMOGRAFÍA DE ESPECIES PIONERAS Y SUCESION SECUNDARIA DE UN BOSQUE TROPICAL HÚMEDO", 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.

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"POR MI RAZA HABLARA EL ESPÍRITU"
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RESUMEN

Con el fin de entender los mecanismos demográficos involucrados en el remplazo entre especies a lo largo del proceso de sucesión secundaria en el bosque húmedo tropical, este trabajo describe la dinámica poblacional de tres especies pioneras (*Trema micrantha*, *Cecropia peltata* y *Trichospermum mexicanum*) a lo largo de las etapas tempranas de la regeneración (primeros 30 años) en parcelas agrícolas abandonadas en Marqués de Comillas, Chiapas. A partir de datos obtenidos del año 2000 al 2014, en parcelas con diferentes edades de abandono, se construyó una crono secuencia para analizar los cambios en la densidad y estructura poblacional, así como en las tasas vitales (reclutamiento, crecimiento y mortalidad) y tasas de crecimiento poblacional (λ) de las tres especies de estudio a lo largo de los años de sucesión. Las especies presentaron diferencias respecto su demografía y dinámica poblacional y estas diferencias estuvieron directamente relacionadas con el gradiente de aparición observado entre las especies de estudio a medida que avanzaba la sucesión. Dicho gradiente inició con *T. micrantha* para la cual el reclutamiento de plántulas estuvo restringido al primer año de sucesión y presentó su mayor densidad en parcelas que tenían menos de un año de abandono. Después de ese pico de abundancia, sus poblaciones declinaron drásticamente, se convirtieron en poblaciones adultas en menos de 10 años, y luego de 14 años no se reportaron más individuos. Siguiendo en el gradiente a *T. micrantha*, las poblaciones de *C. peltata* también presentaron un reclutamiento restringido al comienzo del proceso de regeneración, pero presentaron sus mayores densidades en parcelas que tenían un año de sucesión. Para esta especie, la población permaneció por más tiempo a lo largo de la sucesión, debido a que su densidad declinó de forma más lenta que *T. micrantha*. Luego de más de 20 años sus poblaciones estuvieron conformadas solo por individuos adultos ($DAP \geq 16$ cm), y algunos individuos se reportaron en parcelas que tenían más de 25 años de sucesión. Al final del gradiente *T. mexicanum*

presentó su pico de densidad en parcelas que tenían más de dos años, y fue la única especie con probabilidades de reclutar plántulas en estas etapas sucesionales. Adicionalmente, presentó las tasas de mortalidad más bajas en todas las categorías de tamaño (incluyendo individuos jóvenes), lo que se vio reflejado en una disminución más lenta en la densidad poblacional a lo largo de los años. También se observaron diferencias con las otras dos especies respecto a los cambios en la estructura poblacional, en la cual había individuos juveniles aún en parcelas que tenían más de 10 años, y tomó más de 31 años para que la población estuviera conformada solo por individuos adultos. Además, para el segundo y tercer año de sucesión *T. mexicanum* fue la única especie cuyas poblaciones presentaron valores de $\lambda > 1$, indicando que esta población era la única que estaba creciendo bajo las condiciones de estas etapas sucesionales. Entender los mecanismos involucrados en los procesos de sucesión secundaria en el bosque húmedo tropical, es fundamental para plantear estrategias de manejo y conservación, teniendo en cuenta que la conservación de la biodiversidad de este ecosistema depende en gran medida de la restauración de tierras degradadas, la regeneración de bosques en tierras productivas abandonadas y de la permanencia de bosques maduros.

ABSTRACT

In order to understand demographic mechanisms involved in species turnover during secondary succession process in tropical rainforest, this work describes population dynamics of three pioneer species (*Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum*) during the first years of succession (first 30 years) in old-fields in Marqués de Comillas, Chiapas. We used data gathered from 2000 to 2014, in plots with different ages of abandonment, to build a chronosequence to analyze changes in population density and structure, as well as in vital rates (recruitment, growth and mortality) and population growth rates (λ) of the studied species during succession years. We found that the three species differed in their demography and population dynamics and such differences were directly related with the gradient of appearance observed among study species along secondary succession. The appearance gradient started with *T. micrantha* whose seedling recruitment was restricted to the first year of succession and presented its highest density in plots that were less than one year of abandonment. After that peak of abundance, its populations decreased dramatically, became adult populations in less than 10 years, and after 14 years no more individuals were reported. Continuing the gradient *C. peltata*'s population also faced restricted recruitment at the beginning of the regeneration process, but presented its highest densities in plots that were a year of succession. This species presented a longer period of permanence throughout succession, because its density declined more slowly than *T. micrantha*. After more than 20 years its populations were composed only by old individuals (DBH \geq 16 cm), and some individuals were reported in plots that were more than 25 years of succession. At the end of the gradient *T. mexicanum* presented its maximum density in plots that were over two years old and was the only species likely to recruit seedlings in these successional stages. In addition, it presented lower mortality rates in all size categories (including young individuals), which was reflected in a slower decrease in population density over the years. *T. mexicanum* differed from the other two species also regarding changes in population structure, because for this species there were smaller individuals still in plots that were over 10 years old, and it took more than 31 years old to the population to be composed just by old individuals. *T. mexicanum* was the only one species that presented positive population growth rates ($\lambda > 1$), indicating that this population was the only one that was growing under the conditions of these successional stages. Understanding ecological mechanisms involved in the processes of secondary succession in tropical rainforest is essential to

generate management and conservation strategies, taking in account that conservation of biodiversity in this ecosystem depends largely on restoration of degraded lands, regeneration of forests in old fields and in the permanence of mature forests.

INTRODUCCIÓN

A lo largo de las últimas décadas, la degradación de los ecosistemas naturales ha aumentado principalmente por procesos de transformación directamente ligados con productivas como la agricultura, la ganadería y la extracción de madera (Aide et al., 2013; Rudel & Roper, 1997). En consecuencia, la mayoría de los paisajes en el trópico cálido-húmedo de México, como en otras partes del mundo, se conforman de mosaicos de distintos usos agrícolas del suelo mezclados con vegetación secundaria, remanentes de vegetación primaria y tierras degradadas (Challenger & Dirzo, 2009). Teniendo en cuenta que tanto la deforestación como la fragmentación de los bosques tropicales húmedos (o selvas húmedas) ha sido un factor determinante en la pérdida de la biodiversidad, las funciones y los servicios de estos ecosistemas (Hill et al., 2011), el estudio de los bosques húmedos en paisajes modificados por actividades humanas (PMAHs) se ha vuelto fundamental (Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013).

Sucesión secundaria en campos agrícolas abandonados

Las dinámicas ecológicas de los sistemas naturales tropicales han sido afectadas principalmente por la agricultura, teniendo en cuenta que, por lo menos en el caso del bosque húmedo esta actividad productiva ha sido una de las causas principales de transformación (Gibbs et al., 2010; Quezada, Arroyo-Rodríguez, Pérez-Silva, & Aide, 2014).

La sucesión secundaria en campos agrícolas ocurre cuando por diferentes razones sociales (e.g. migración), económicas (e.g. falta de subsidios) y ecológicas (e.g. agotamiento del suelo), las tierras agrícolas se abandonan abriéndose espacios donde el bosque puede regenerarse de manera natural (Chazdon, 2014; Ostertag & Guariguata, 2001). Las trayectorias sucesionales en estos campos agrícolas abandonados dependen de una gran cantidad de variables (tabla 1) que actúan directa o indirectamente de forma simultánea a

diferentes escalas espaciales (Arroyo-Rodríguez et al., 2017). Adicionalmente, la historia de manejo tiene un efecto directo sobre dichas variables (Chazdon, 2003; Norden, Mesquita, Bentos, Chazdon, & Williamson, 2011) lo cual hace de la sucesión secundaria en estos sistemas un proceso complejo y poco predecible (Norden et al., 2015) . Por lo tanto, comprender en detalle los mecanismos ecológicos que determinan los procesos de regeneración natural y sucesión secundaria en los bosques húmedos tropicales intervenidos es fundamental para poder establecer estrategias de manejo y conservación de la biodiversidad dentro de los PMAHs (Chazdon et al., 2009).

Tabla 1. Variables directas e indirectas a diferentes escalas espaciales que determinan la sucesión secundaria en bosques húmedos tropicales (modificado de Arroyo-Rodríguez et al., 2017)

ESCALA ESPACIAL			
VARIABLES	Local	Paisaje	Regional
Variables directas	<ul style="list-style-type: none"> -Fuente de propágulos (semillas, fustes) -Propiedades del suelo -Microclima -Interacciones bióticas 	<ul style="list-style-type: none"> -Dinámica poblacional de dispersores, polinizadores y herbívoros -Meso clima -Invasiones biológicas 	<ul style="list-style-type: none"> -Acervo de especies nativas y exóticas (plantas y animales) -Especiación y extinción -Migración
Variables indirectas	<ul style="list-style-type: none"> -Régimen de disturbios -Forma y tamaño del fragmento -Aislamiento del fragmento 	<ul style="list-style-type: none"> -Cobertura de bosque -Características de la matriz -Conectividad del paisaje -Cantidad total de borde en bosque -Cantidad total de núcleo de bosque 	<ul style="list-style-type: none"> -Clima -Topografía -Disturbios naturales

Sucesión como un proceso jerárquico

La sucesión secundaria en campos agrícolas abandonados puede entenderse como un proceso a nivel de comunidad, en el cual, se da la colonización y el remplazo de grupos funcionales de especies arbóreas que se diferencian respecto a sus historias de vida (Huston & Smith, 1987). Por lo general, se ha propuesto que este proceso es el resultado de una serie de interacciones bióticas (e.g. competencia inter e intra específica) que son dictadas por gradientes de condiciones y disponibilidad de recursos que cambian, horizontal y verticalmente, a medida que el bosque se desarrolla (Horn, 1974).

Estas interacciones tienen un efecto directo sobre las tasas de reclutamiento, crecimiento y mortalidad de las poblaciones de las especies presentes en un momento dado del proceso sucesional. Por lo tanto, en parte, determinan el cambio temporal en la estructura y composición de las comunidades. (Marcante, Winkler, & Erschbamer, 2009; van Breugel, Bongers, & Martínez-Ramos, 2007). Así, desde un enfoque jerárquico la sucesión secundaria puede entenderse como un proceso en el cual los procesos a niveles ecológicos superiores (comunidades) pueden explicarse como el resultado de procesos que ocurren en niveles inferiores (poblaciones) (Falinska, 1993; Peet & Christensen, 1980).

Historias de vida y sucesión secundaria

Las diferencias en las historias de vida son uno de los factores clave para entender el remplazo entre especies a lo largo de la sucesión. De hecho, la clasificación más general de especies arbóreas involucradas en los procesos de regeneración de bosques, se basa en historias de vida contrastantes (Swaine & Whitmore, 1988). Siguiendo esta clasificación, por un lado, están las especies pioneras, que son especies de vida corta que sólo pueden establecerse en claros grandes con elevada disponibilidad de luz y cuyas plántulas no prosperan bajo la sombra del dosel. Por el otro, están las especies no pioneras (o de vegetación primaria), que son de vida larga, las cuales tienen semillas que germinan en la sombra y cuyas plántulas y árboles juveniles pueden crecer bajo sombra. Swaine y

Whitmore (1988) sugieren que, dependiendo del grado de perturbación, los procesos de sucesión implican un recambio continuo de especies con diferentes grados de tolerancia a la sombra, con las pioneras extremas iniciando la sucesión y las especies no pioneras más tolerantes a la sombra terminándola. A pesar de que esta clasificación ha sido muy útil para tener una idea general de los cambios en la comunidad a lo largo de la sucesión (Finegan, 1984), está basada en patrones demográficos generales y subestima la gran variabilidad demográfica de los árboles tropicales (Martínez-Ramos, Alvarez-Buylla, & Sarukhán, 1989).

Los procesos exitosos de colonización se relacionan con la supervivencia diferencial, el crecimiento y la reproducción de las especies (Martínez-Ramos et al., 1989). Por lo tanto, es posible que la existencia de una amplia diversidad de especies pioneras en las selvas húmedas tropicales (Brokaw & Scheiner, 1989; Martínez-Ramos, 1985) sea producto de la variabilidad demográfica que hay entre dichas especies, lo que a su vez permite su coexistencia. Se ha demostrado que en las primeras etapas de la sucesión en bosques tropicales puede darse el remplazo entre especies con estrategias similares debido a diferencias en propiedades demográficas, tales como el reclutamiento y la mortalidad (Mesquita, Ickes, Ganade, & Williamson, 2001; van Breugel et al., 2007), lo cual puede repercutir directamente en la estructura de las comunidades de los bosques secundarios (van Breugel, van Breugel, Jansen, Martínez-Ramos, & Bongers, 2012).

La mayor parte de los estudios que han descrito cambios en la demografía de las especies a lo largo de la sucesión se han enfocado en contrastar la dinámica poblacional de especies que participan en diferentes momentos de la sucesión (pioneras versus especies tolerantes) (Marcante et al., 2009; Martínez-Ramos et al., 1989; Primack & Lee, 1991) o en evidenciar los cambios de la demografía de una misma especie a medida que el bosque se desarrolla (Otárola & Avalos, 2014; Pascarella et al., 2007; Valverde & Silvertown, 1998). Por ello, son pocos los estudios que muestren las diferencias demográficas que pueden existir entre especies que participan en una misma etapa sucesional. Analizar las diferencias demográficas que presentan las especies pioneras es una herramienta clave para entender

los mecanismos involucrados en el remplazo de especies en las primeras etapas de la sucesión.

El presente proyecto busca comprender en qué medida las diferencias entre las historias de vida de las especies pioneras influyen en la posición que éstas ocupan dentro del gradiente de remplazo a lo largo de las primeras etapas del proceso de sucesión secundaria (primeros 30 años). Para ello, se tomaron como caso de estudio tres especies pioneras comunes de selvas húmedas de México con el fin de identificar en qué grado se diferencian sus historias de vida y su dinámica poblacional (tomando como base su estructura poblacional y sus estrategias reproductivas) a lo largo de las primeras etapas del proceso de sucesión secundaria. Las especies analizadas fueron *Trema micrantha*, de aquí en adelante llamada *Trema*, *Cecropia peltata*, de aquí en adelante nombrada *Cecropia* y *Trichospermum mexicanum*, de aquí en adelante llamada *Trichospermum*.

Tabla 2. Atributos reproductivos de *Trema*, *Cecropia* y *Trichospermum*

Especie	Masa de semillas (mg)¹	Tipo de diáspora	Tipo de dispersión²	Modo reproductivo^{2,3}	Banco de semillas³	Tipo de germinación⁴
<i>Trema</i>	2,8	Fruto	Zoócora	Masivo y continuo	Banco de semillas de corta duración	Fotoblástica
<i>Cecropia</i>	1	Fruto	Zoócora	Masivo y continuo	No hay acumulación de semillas	Fotoblástica
<i>Trichospermum</i>	2,5	Semilla	Anemócora	Época seca	Banco de semillas de larga duración	Termoblástica

Fuentes:

1-Lohbeck, 2014

2-Ibarra-Manríquez et al, 1991

3-Martínez-Ramos et al., 2016

4-Pearson et al., 2002

Tabla 3. Atributos funcionales de *Cecropia*, *Trema* y *Trichospermum*. Abreviaciones: AF: área foliar, AFE: área foliar específica, CMS: contenido de masa seca. GF: grosor foliar, DM: densidad de madera; TCA: tasa de crecimiento altura. DE: densidad estomatal; N: contenido de nitrógeno, P: contenido de fosforo.
Fuentes:

Especie	AF (cm ²)	AFE (cm/gr)	CMS (ps (mg)/pf (g))	GF (mm)	DM (gr/cm ³) ³	TCA (m/año) ⁴	DE ⁵	N (mg/g) ⁵	P (mg/g) ⁵
<i>Cecropia</i>	2506,0 ¹	141,100 ¹	381,298 ¹	0,164 ¹	0,240	3-5	142	22,08	1,22
<i>Trema</i>	55,0 ¹	212,6 ¹	285,1 ¹	0,18 ¹	0,28	7	496	22,93	1,51
<i>Trichospermum</i>	84,9	166,6 ²	378,1 ²	0,17 ²	0,24	-	299	18,06	1,11

1- Lohbeck, 2014

2-Tauro, 2003

3-Parcelas en bosque primario establecidas en Chajul. Elizabeth Schüller, Peter Heitz and Miguel Martínez-Ramos data. Datos no publicados

4-Brokaw, 1987

5-Bongers & Popma, 1990

Las tres especies presentan algunas similitudes respecto a sus estrategias reproductivas y de colonización (Tabla 2), así como respecto algunos rasgos funcionales de sus hojas (Tabla 3). Dichas características permiten que sean especies adaptadas para participar en las primeras etapas de la sucesión, teniendo en cuenta los altos niveles de luz que requieren para el establecimiento de semillas y plántulas, y la capacidad de sus hojas para realizar fotosíntesis a tasas elevadas, permitiéndoles tasas de crecimiento rápidas. Sin embargo, las diferencias sutiles que presentan respecto a estos aspectos pueden reflejarse en dinámicas poblacionales diferentes a lo largo de la sucesión, dando como resultado un gradiente de remplazo.

Teniendo en cuenta que son especies pioneras de un mismo ecosistema, se espera que las tres especies compartirán ciertas características generales de su demografía. Sin embargo, su posición dentro del gradiente de remplazo será distinta a lo largo de las primeras etapas de la sucesión secundaria, como consecuencia de las diferencias en sus estrategias reproductivas y de colonización. Se espera que el remplazo ocurra en el orden

Trema ► *Cecropia* ► *Trichospermum*, considerando que *Trema* presenta tasas de crecimiento relativamente más altas que las otras especies y germinación fotoblástica, permitiéndole un mayor reclutamiento al inicio de la sucesión. Posteriormente ingresará en el proceso de colonización *Cecropia*, cuyo reclutamiento demanda menos cantidades de luz y, por último, colonizará *Trichospermum* pues presenta tasas de crecimiento menores a las otras dos especies, la germinación de sus semillas no es estrictamente fotoblástica, y estas pueden permanecer durante más tiempo en el banco de semillas.

Sobretiro Artículo científico enviado

Demographic differentiation among pioneer tree species during old-field succession of a Neotropical rainforest

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Head short title: Demographic differentiation of pioneer species along secondary succession

SUMMARY

1. Early pioneer species share life history attributes enabling them to colonize disturbed sites, but how much they differ demographically and how such differentiation determines pioneer species turnover during succession are still open questions. Here, we approached these issues by comparing demographic patterns and population dynamics of three dominant pioneer tree species during the old-field succession of a tropical rainforest at Southern Mexico.

2. We combined chronosequence (1 to 30 years of abandonment) and long-term (from 2000 to 2014) dynamic approaches to assess changes in population structure, stage-specific vital rates (survival, growth, and fecundity), and population growth rate (λ) of the pioneer species *Trema micrantha*, *Cecropia peltata*, and *Trichospermum mexicanum* during the first 30 years of succession.

3. *Trema* colonized first and had the shortest life span (< 10 years), followed by *Cecropia* (< 28 years) and *Trichospermum* (> 31 years). All species exhibited hump-like successional trajectories of population density, with *Trema* reaching a peak in density during the first, *Cecropia* along the second, and *Trichospermum* after the third year of succession. After these peaks, *Trema* exhibited faster negative population growth rate ($\lambda = 0.567-0.720$) than *Cecropia* ($\lambda = 0.766-1.013$), while populations of *Trichospermum* were still increasing in size ($\lambda = 1.009-1.635$). Recruitment and survival rates of seedlings and juveniles defined the period of population increase and the successional year of maximum density of each species. Mortality rate in mature stages determined the residence time of species during

succession. An important variation in species replacement occurred among secondary forest stands. In some stands *Trema* was abundant and *Cecropia* almost absent, while in others it was the opposite or both species were similar in abundance. We inferred that priority inhibitory effects operate on these species during the colonization of open fields.

4. *Synthesis*: Although *Trema*, *Cecropia*, and *Trichospermum* are classified as typical pioneer trees, these species differed importantly in their population dynamics during succession. Different levels of shade intolerance in the seedling and juveniles stages determined replacement between these species, but inter-specific priority inhibitory effects during field colonization may also be involved in this process. Our study shows that detailed demographic analysis significantly adds to the understanding of old-field tropical rainforest succession.

Key words: *Cecropia*, *Trema*, *Trichospermum*, Matrix models, Selva Lacandona, plant demography

1 INTRODUCTION

Already more than four decades ago, it was recognized that we are living in the era of secondary vegetation (Gómez-Pompa & Vázquez-Yanes, 1974). Today, old-growth forests cover smaller areas than second-growth forests (*sensu* Chazdon, 2014) in most regions on earth (Brown & Lugo, 1990; Turubanova, Potapov, Tyukavina, & Hansen, 2018).

Deforestation, land use change towards agriculture, field abandonment, and ecological succession are the main forces driving this ongoing transformation (Aide et al., 2013; Hansen et al., 2013). In this context, second-growth forests are becoming keystones for conservation of biodiversity, ecosystem functioning and services (Chazdon et al. 2016, Poorter et al. 2016, Rozendaal et al. 2019). Therefore, there is an urgent need to understand ecological processes and mechanisms determining natural regeneration and successional dynamics of second-growth forests, especially in abandoned agricultural fields (Chazdon, 2014).

Secondary succession can be understood as a process of turnover among species differing in life history and functional traits, which is initiated by a disturbance (Halpern, 1989; Huston & Smith, 1987). Such differences determine the species ability to survive, grow and reproduce in an environment that changes dynamically along time in abiotic conditions, resources, and biotic interactions (Arroyo-Rodríguez et al., 2017; Horn, 1974; Martínez-Ramos, 1985). This changing environment affects the species population dynamics and this, in turn, results in species replacement through time (van Breugel, Martínez-Ramos, & Bongers, 2006).

Often, life-history strategies of tropical rainforest tree species are dichotomously categorized into pioneers and non-pioneers (Swaine & Whitmore, 1988). Pioneer species (or light demanding) are considered short-lived, with early maturation, fast growth, and high reproduction rates, which establish only in open areas. Non-pioneer species (or shade-tolerant) are long-lived, with late maturation, slow growth, and low reproduction rates, which establish under shade conditions. Although this classification is useful to assess community changes along succession (Finegan, 1984) it is based on general (average) demographic patterns and dismiss the high demographic variability found among tropical tree species (Martínez-Ramos, Álvarez-Buylla, & Sarukhán, 1989; Poorter et al., 2008). In fact, pioneer and non-pioneer species represent the ends of a wide spectrum of life histories and regeneration strategies (Hubbell, 2005; Martínez-Ramos, 1985). The demographic exploration of such variability is core for understanding processes of natural regeneration and old-field forest succession.

Community oriented studies have shown that old-field succession in the tropics is not an easily predictable process (Norden et al., 2015). Replacement not necessarily occurs among tree species with contrasting life histories (e.g. non-pioneer replacing pioneer species), but also among species with similar life histories (e.g. pioneer replacing pioneer species; Brokaw, 1987; Mesquita, Ickes, Ganade, & Williamson, 2001; van Breugel, Bongers, & Martínez-Ramos, 2007). This suggests a fine niche partitioning among species during early succession. Detailed demographic analysis of the species can help to explore such partitioning process (Finegan, 1984; Metcalf, Horvitz, Tuljapurkar, & Clark, 2009; Silvertown & Franco, 1993). However, most demographic studies in successional systems have focused on species that dominate at different moments of succession (Marcante,

Winkler, & Erschbamer, 2009; Martínez-Ramos et al., 1989; Primack & Lee, 1991), or on changes in vital rates of a single species during succession (Otárola & Avalos, 2014; Pascarella et al., 2007; Valverde & Silvertown, 1998). Comparative studies of the demographic behaviour of different pioneer tree species during succession are scarce (Brokaw, 1987; T. R. H. Pearson, Burslem, Goeriz, & Dalling, 2003b; Santos, Santos, Nascimento, & Tabarelli, 2012). Thus, the question of how pioneer species replace each other during first stages of old-field succession is still open.

In this study we explored demographic mechanisms underlying replacement of pioneer tree species during the first stages of the old-field succession of a tropical rainforest. We aim to assess how differences in life history, vital rates, and population growth rates among pioneer species explain their position during succession. As case study, we used three pioneer species (*Trema micrantha*, Ulmaceae; *Cecropia peltata*, Cecropiaceae; and *Trichospermum mexicanum*, Tiliaceae), which are dominant (in abundance and biomass) during the first 30 years of old-field forest succession at Southern Mexico (van Breugel et al., 2007). Although these species belong to different phylogenetic floristic families, they have similar regeneration strategies and functional traits (Table S1 and S2, Supporting information). Specifically, we addressed the following questions: 1) to what extent do population density and size structure, stage-specific vital rates (survival, growth and reproduction), and dynamics (finite population growth rates) differ among pioneer species during the first year of the successional process? 2) Do these demographic differences explain the replacement order among pioneer species during succession? We predict a gradient species replacement sequence going from the species having the highest growth and mortality rates to the species with the lowest rates.

2 MATERIAL AND METHODS

2.1 Study site

The study was conducted in the region of Marqués de Comillas (MdC), southeast Mexico (16°04' N, 90°45' W). Average annual rainfall is about 3000 mm, and the mean monthly temperature is about 22°C (Martínez-Ramos, Anten, & Ackerly, 2009). Dominant vegetation is lowland tropical rainforest, which structure and composition change across different geomorphological units (Ibarra-Manríquez & Martínez-Ramos, 2002; Navarrete-Segueda et al., 2017). The region has witnessed a fast forest conversion to agriculture and presently near 30 percent of landscape is covered by second-growth forest of different ages, resulted from the abandonment of crop and pasture fields (Carabias, de la Maza, & Cadena, 2015; Martínez-Ramos et al., 2016). This landscape composition has allowed successional studies of communities of plants and animals in chronosequences of second-growth forests (e.g. Hernández-Ordóñez, Urbina-Cardona, & Martínez-Ramos, 2015; van Breugel et al., 2006).

Trichospermum mexicanum (hereafter referred to as *Trichospermum*) is one of the most abundant pioneer tree species in secondary vegetation in humid tropical areas of México, reaching 20-m height and 50-cm of diameter at breast height (DBH; Pennington & Sarukhán, 2005). This monoecious tree produces dehiscent bivalve capsules with a mean of 11 wind-dispersed ciliate seeds, which are produced during the dry season (Rodríguez-

Velázquez, Sinaca-Colín, & Jamangapé-García, 2009). *Cecropia peltata* (hereafter referred to as *Cecropia*) is a very abundant and conspicuous pioneer species in tropical rainforest, reaching 20 to 35-m height and 50-cm DBH. As other *Cecropia* species, this dioecious species produce small seeds which are dispersed by several birds, bats and arboreal mammals (Estrada, Coates-Estrada, & Vázquez-Yanes, 2010), and its stems are colonized by Azteca ants (Alvarez-Buylla & Martínez-Ramos, 1992). *Trema micrantha* (hereafter referred to as *Trema*) is a very abundant pioneer species with wide distribution in the Neotropics. This tree reaches 15-20 m height and 30-cm DBH and has fleshy fruits eaten by birds (Pennington & Sarukhán, 2005). Other life history and functional attributes of the studied species are shown in Table S1 and S2 (Supporting information).

2.2 Study system

Between 2000 and 2014, we established in MdC a study system composed by thirteen abandoned cornfields with initial fallow ages varying between 0 to 17 years (Fig S1, supporting information). This fallow age range is representative for the second-growth forests in the study region. All fields had similar land use histories (Table 1). Due to land use history and dynamics in the region, numbers of sites were unbalanced regarding fallow age, with very few sites recently abandoned (less than 1 year), more sites between 1 and 10 years, and few sites older than 15 years. In each field, we established a permanent plot of 10 m × 50 m. In these plots, we followed different sampling protocols for each life-cycle stage to gather demographic data useful to answer our research questions, as following described.

Seed bank.- To estimate density of seeds in the soil we used two plots (R-1 and H-1(table 1)). In each plot, twenty soil samples were randomly collected with a metallic core (10-cm diameter x 10-cm depth; total sampled area = 0.20 m²). Sampling was conducted in two dates (one in the dry season and other in the rainy season). Each soil sample was spread in individual trays with sterile soil, which were put on tables inside a rustic shade-house covered with a transparent plastic mesh. This cover ensured a high level of light for the germination of these light-demanding seeds. The number of emerged seedlings of the three studied species was recorded daily for three months, until no more seedlings emerged.

Seed rain.- In plots R-1 and H-1, we established 12 conical traps (0.5 m radius and 0.5 m deep, each), established 1-m above ground, to record seed rain of the studied species. Litter was collected from each trap every two weeks. In the laboratory, samples were sorted to separate and count the seeds per species, trap, and date with the help of a magnifying glass.

Seedlings and small juveniles.- In each of four plots (R-0, H-0, R1, and H-1), we established 12 sub-plots of 1×2-m each (total 48 subplots) where all seedlings (individuals with 5 to 50-cm height) and small juveniles (51 to 149-cm height) of the three studied species were recorded, tagged and measured in height. At intervals of about 3-4 months, we recorded surviving individuals and new recruits (new emerged seedlings) and measured them in height.

Large juveniles and mature individuals.- For individuals with heights ≥ 1.5 m we did annual censuses conducted in the total area of each of our 13 study-plots (see above). All individuals of each species were inventoried, tagged with an individual number, and measured in DBH. At each census, we recorded DBH of surviving trees and of new recruits (i.e., those individuals reaching 1.5 m height).

Reproductive schedule. - For *Cecropia* and *Trichospermum*, in July 2017 we selected 24 and 35 potentially reproductive individuals, respectively, covering a size range of 6 to 40 DBH, to estimate size-specific fecundity rates (i.e. seeds production per tree per year). These individuals were located outside our study plots, on patches of second-growth forest and along trails. From July 2017 to July 2018, we recorded on a monthly basis the reproductive stage (with or without fruits) of each individual. We estimated the number of produced seeds per tree during one year, following the protocol described in the Supporting information. For *Trema* we did not estimate fecundity because it was not possible to find enough mature individuals, both within and outside the plots.

2.3 Data analysis

Change in population density and population structure during succession.- We used data gathered from each of our 13 study plots along the census years (Table 1). For each species, and year by year, we calculated the mean population density (number of individuals in 0.05 ha) among plots of the same fallow age (for more details see Appendix 2, Fig. S1). In this analysis only individuals with ≥ 1 -cm DBH were included, as these individuals suffered low mortality rates ($< 10\%$ year) and can be considered established in the population.

To assess changes in population structure, individuals of each species were assigned to one of the eight life stage categories: Seedlings (from 10 cm to 50 cm height), Juveniles-1 (51 to 149 cm height), Juvenile-2 (150 cm height and ≤ 1 cm DBH), Juveniles-3 (1-2 cm DBH), Pre-matures (2-4 cm DBH), Matures-1 (4-8 cm DBH), Matures-2 (8-16 cm DBH) and Matures-3 (> 16 cm DBH). These categories encompass the main life-cycle stages of the species. Because individuals at different life stages were censused in sampling areas of

dissimilar size, we scaled abundance of every category to a standard area of 1 ha. Then, for plots with same fallow age, we summed the number of individuals per life stage category, and the population size structure of each species was described as the proportion of the population at the different size categories. Finally, we assessed the change of population size structure among different fallow ages.

Estimation of vital rates of the species.- Stage-specific survival, growth, and fecundity rates were estimated for each species considering trees with $DBH \geq 1$ cm. For stage-specific survival rate, we combined DBH records of all surviving or dying individuals from one year to the next, across all permanent plots and monitored years. This produced a large list of individuals with their DBH and surviving condition (live =1, dead = 0). Due to the repeated measure nature of this data (i.e., DBH and surviving condition of same individuals were recorded along years) and to minimize possible bias due to very large degrees of freedom, we decided to use average survival probabilities per small DBH categories, instead using individual records. For this, individuals were categorized into DBH classes of 2-cm and the average of zeros (dead) and ones (survivors), which is equal to the mean annual survivorship probability, was obtained for each category. Same procedure was applied to estimate stage-specific growth rates, except that in this case, instead of survival condition, we used the relative growth rate (RGR) of each living individual. RGR was calculated as $[\text{Log}(DBH_1) - \text{Log}(DBH_0)]/t$, where DBH_0 is the tree diameter at the beginning of an annual interval, DBH_1 is the diameter at the end of that interval, and t is a time interval (in our case one year). Stage-specific fecundity rates were estimated using the seed production records we gathered from the trees of *Cecropia* and *Trichospermum* monitored for one year (see previous section and supplementary information). We used the

maximum seed production value recorded for each sampled individual during the year as an estimator of fecundity, and calculated mean fecundity rate per 2-cm DBH classes, as was done for survivorship and growth rates. Finally, we used generalized linear models (GLM), considering a normal error and an identity link function, to assess differences in stage-specific survival (angular transformed), growth, and fecundity (log-transformed) rates among studied species. We fitted different models (linear, exponential, semi-log, and potential) and selected those maximizing the proportion of explained variance (R^2). In these models, each of these vital rates (survival, growth and fecundity) was the response variable, while the species (a factor with three levels) and the mid-point of 2-cm DBH classes (a continuous variable) were the explanatory variables. We used the interaction species x DBH to test differences in the curve intercept (i.e., vital rate value when DBH = 1 cm) and curve slope (i.e., the speed of change of a given vital rate as DBH increases).

Population flux models. We lumped demographic data obtained from four of our 13 plots (R-0, H-0, H1 and R-1) to construct population flux models for each species, which describes stage-specific transition probabilities (progression, permanence, retrogression, mortality and fecundity) along all life-cycle stages. Besides the above-mentioned stage life categories, in these models we included seed rain and seed bank stages. The models were separately constructed for the second and the third years of succession. Only for those years we had all the demographic data required to estimate the whole set of stage-transition probabilities for our three studied species. Stage-specific permanence rates (stasis probability) were calculated as the proportion of surviving individuals that remained in the same stage during one successional year. Stage-specific mortality rates were calculated as the proportion of individuals of a given stage dying during one successional year. Stage-

specific progression rates were calculated as the proportion of surviving individuals of a given stage that grew enough to reach following stage(s) during one successional year. Retrogression probabilities was estimated as the proportion of those living individuals returning to previous stages, due to the rupture of the trunk and regrowth or ? loss of one more stems in multi-stemmed individuals. Permanence and mortality rates of soil seeds was estimated using records provided in the literature (Alvarez-Buylla & Martínez-Ramos, 1992; Dalling, Swaine, & Garwood, 1997). As we did not have the data to calculate directly the progression rate between the seed and seedling stages, we estimated this transition dividing the number of available seeds in a year (summing seed rain and seed bank) by the number of new seedlings that emerged during each successional year. In the models seed rain density corresponded to the total number of seeds trapped per year in plots H-1 and R-1 and scaled to one hectare. Seed bank density corresponds to the mean number of emerged seedlings from the two-soil sampling dates in the R-1 and H-1 plots and scaled to one hectare. These data corresponded to the third successional year. Because we did not have soil samples for the second year of succession, in the models we used the same mean soil seed density for that year period. Stage-specific fecundity rates were quantified using the fecundity-DBH model described in the previous section. To do this, with this model we estimated annual fecundity of each mature individual (recorded in the R-0, H-0, H1, and R-1 plots) based on its DBH in each of the two studied successional years, and fecundity rate for each mature category was calculated averaging fecundity values of all individuals belonging to that category.

Estimation of population growth rate of the species. To obtain estimates of the finite population growth rate (λ) for each species, we translated the flux population models above

described into Lefkovich matrix projection models (Caswell, 2001). We used the same stage categorization of previous analysis, except for the Matures stage, which was created by combining data of all reproductive stages (Matures 1, 2 and 3) to increase sample size. As we did not have reproductive data from *Trema*, for this species we used fecundity values of *Cecropia* (similar reproductive behaviour), to build the matrix. The used model has the form $\mathbf{n}(\mathbf{t}+1) = \mathbf{A} \times \mathbf{n}(\mathbf{t})$, where \mathbf{A} is a square matrix containing the contributions of individuals in the j -th stage to the i -th stage in one-time step (in our case one year), $\mathbf{n}(\mathbf{t})$ is a vector representing the density of individuals in the i -th stage at time \mathbf{t} , and $\mathbf{n}(\mathbf{t}+1)$ is a vector representing the density of individuals in the i -th stage in time $\mathbf{t}+1$. We estimated λ and its confidence intervals (CIs) for each species and successional year using a Monte-Carlo bootstrap resampling procedure, as described in Caswell (2001). In this method, each observation in the bootstrap is one individual and its corresponding transition rates. In each run of the bootstrap, one observation per size class was randomly sampled with replacement for a total of ten observations resampled per run. The remaining observations were used to construct matrix \mathbf{A} . We then used a numerical, iterative, technique for estimating λ (Caswell, 2001). Each value for λ was obtained after 256 iterations, which ensured to have a stable λ value. This was repeated 1000 times to have a large bootstrap distribution of λ values. Finally, from this distribution we got 5% and 95% percentiles as confidence intervals. Finally, to assess the relative contribution of each stage-specific transition probabilities to λ , we carried out elasticity analysis (see details in de Caswell, 2001). Elasticity measures the relative effect of a proportional change in a given transition probability on λ (de Kroon, Plaisier, van Groenendael, & Caswell, 1986).

3 RESULTS

3.1 Successional changes in population density and population structure

All species shared a similar trajectory of change in population density during succession. Population density increased to a maximum and then decreased rapidly (Fig. 1). However, species differed in the successional time at which they reached their maximum density. *Trema* had a peak of density (mean \pm SE: 61 ± 61 in 0.05 ha) in the first year, *Cecropia* (180.4 ± 156.7) during the second year, and *Trichospermum* (119.5 ± 73.2) during the third year of succession. Also, the species differed in the rate at which population density decreased during succession. *Trema* decreased very fast and eight years after field abandonment its density was practically zero (~ 1 ind/ha). The decline of *Cecropia* was also fast but some individuals were recorded in plots with more than 20 years of succession. *Trichospermum* decreased at the slower rate and was the only species with individuals in plots with fallow ages more than 30 years. *Trema* declined very fast when *Cecropia* reached its maximum density and occurred with *Cecropia* when *Trichospermum* reached its peak of density (Fig. 1 inset).

Population density of the three species exhibited high variation among plots of same successional age, especially during the first years (Fig. S2. supporting information). Interestingly, in plots where *Cecropia* had high population densities *Trema* showed very low densities and vice versa. On the other hand, some plots (e.g., R-0, H-1 and S-8) showed a clear species replacement among the three pioneer species (Fig. S2).

Population structure differed notoriously among species during succession (Fig. 2). The population structure of *Trema* changed rapidly during the first 10 years of succession,

from being dominated by juvenile trees (smaller than 2-cm DBH) to a population composed only by large trees (DBH \geq 16 cm). Such change did take 22 years in *Cecropia* and more than 31 years in *Trichospermum*. In other words, *Trema* population “got older” and disappeared during succession at a faster rate than *Cecropia* and *Trichospermum* was the slowest. Only *Trichospermum* had young individuals (< 1-cm DBH) after 10 years of succession.

3.2 Interspecific differences in size-specific vital rates

In all species, survivorship rate increased with DBH, with *Trema* and *Cecropia* exhibiting the lowest survival rates at the smaller sizes and the faster increase in survival with DBH (Fig. 3). In all species relative growth rate (RGR) decreased with DBH, with *Trema* showing the higher RGR in almost all sizes and the faster decay in RGR as size increased. *Cecropia* and *Trichospermum* showed practically the same decreasing trajectory of RGR with DBH. Fecundity rates increased in an exponential way with DBH in *Cecropia* and *Trichospermum*, but fecundity for same size was three to 10 times higher in *Cecropia* than in *Trichospermum* (Fig. 3).

3.3 Population flux models and population growth rates

Stage-specific transition probabilities differed among the three studied pioneer species in the same successional year, and for same species between successional years (Fig. 3). In all species seedling density was more than two orders of magnitude smaller than seed density (seed rain plus seed bank). In concordance, the progression probability between the seed and seedling stages was very low or null; in fact, only *Trichospermum* showed a probability different from zero in the second successional year. Overall, across life-cycle stages and

successional years, *Trema* showed the highest stage-specific mortality rates and *Trichospermum* the lowest ones. *Trema* showed a strong limitation in the progression transition between seedling and juvenile stages due to a very high mortality rate (near 100% per year). A similar situation was observed for *Cecropia* but in a less degree. *Trichospermum* showed the lowest stage-specific mortality rates and highest progression probabilities in both successional years. In the third successional year, these demographic differences among species become wider (Fig. 3).

During the second year of succession, some juvenile individuals of *Cecropia*, but particularly of *Trichospermum*, grew very fast transiting more than one life stage in a year. For the third year of succession, only individuals of *Trichospermum* showed such behaviour. Also, juvenile and mature individuals of both species exhibited retrogression rates, which resulted from stem damages caused by falling branches or the loss of one or more stems in multi-stemmed trees. Finally, the *Cecropia* population produced two to four times more seeds than that of *Trichospermum* in both years, which was due to the much higher size-specific fecundity rates of the former species (Fig. 3).

For the three species, estimates of population growth rate (λ) were significantly higher for the second than for the third year of succession. *Trichospermum* exhibited the highest λ values in both successional years, and it was the only species with an increasing population ($\lambda > 1$) in the two successional years. Conversely, both *Trema* and *Cecropia* showed decreasing populations ($\lambda < 1$), the former species having a faster population decreasing rate than the latter. For the three species and the two studied annual periods all elasticity was concentrated (elasticity = 1) in permanence of the bigger mature stage (data not shown).

4 DISCUSSION

Our results show that the studied species, although classified as early successional pioneer trees, differ importantly in their demographic attributes, time of maximum density during succession, and longevity. *Trema* was the first colonizer and showed the smallest longevity (< 10 years), followed by *Cecropia* (< 28 years), and finally by *Trichospermum* (> 31 years). Such positions during succession paralleled the replacement process between pioneer species reported in previous community level studies at our study system (van Breugel et al., 2007).

Dispersal and establishment limitation, temporal fluctuations in recruitment processes, and negative-density dependence are some major factors determining population size and dynamics of tropical rainforest tree species during old-field succession (Arroyo-Rodríguez et al., 2017; Norden et al., 2015). The replacement among pioneer species can be associated with interspecific differences in the strength with which these ecological forces operate on populations during succession (Chazdon et al., 2007; Falinska, 1993; Halpern, 1989). Despite the fact that pioneer species share similar life histories (Table S1) they differ in some of their requirements for seed dispersal, seed germination, seedling establishment and in the levels of light resources needed for recruitment, survival, and growth (Dalling & Hubbell, 2002; Dalling, Winter, & Hubbell, 2004; Pearson, Burslem, Goeriz, & Dalling, 2003a).

4.1 Seed availability and dispersal limitation

Two years after field abandonment, there was a high density of seeds of the three pioneer species, both in the seed rain and in the seed bank (Fig. 4). In recently opened fields seeds

can come from nearby trees (Finegan, 1984) or from the soil seed bank (Lopez-Toledo & Martínez-Ramos, 2011; Quintana-Ascencio, Gonzalez-Espinosa, Ramirez-Marcial, Dominguez-Vazquez, & Martinez-Ico, 1996). It is well known that the pioneer species studied here produce abundant crops of small seeds which are widely dispersed by animals (*Trema*, *Cecropia*) or by wind (*Trichospermum*) (Alvarez-Buylla & Martínez-Ramos, 1992; Ibarra-Manríquez, G; Sánchez-Garfias B; González-García, 1991; Rodríguez-Velázquez et al., 2009). Based on our results, we believe that at the time of field abandonment seed availability was not a limiting factor for colonization of any of the studied species. During the second year of succession, seed rain density of the three species was almost two-fold higher than the seed bank density, but in the third year seed rain density decreased in all species, and the seed bank became the most important source of propagules (Fig. 4). Whether these changes were due to effects of inter-annual variation in climate conditions on seed production or by effects of increasing levels of intra and inter competition needs further studies.

4.2 Seedling recruitment and establishment limitation

Our results indicate that the temporal window for seedling emergence and recruitment after field abandonment was very short and differed among the studied pioneer species. For *Trema* this window was restricted to the very beginning of succession as no new seedlings were recorded one year after field abandonment (Fig. 4). The same result was observed for *Cecropia*, while for *Trichospermum* new seedlings were recorded still r two years after succession had started. Such seedling recruitment behaviour has been reported for *Trema micrantha* and for *Cecropia insignis* (a close congeneric of *Cecropia peltata*) after forest

gap formation (Brokaw, 1987). Also, it has been reported that seedling recruitment of *Cecropia* is restricted to the first two year after roadside disturbance (Fleming & Williams, 1990). Seeds of these species require high red/far-red light ratios (*Cecropia*) or high temperature fluctuations (*Trema*) to germinate (Pearson, Burslem, Mullins, & Dalling, 2002; Válio & Scarpa, 2001; Vázquez-Yanes & Smith, 1982). Thus, seedlings recruitment in these species is expected to be strongly limited once a forest canopy is formed. Other studies conducted in our study system have shown that light availability in the understory declines very fast during succession, and after 10 years of succession the photosynthetic active radiation at 1 m above ground is similar to that in the old-growth forest (Ricaño-Rocha, 2007). Conversely, *Trichospermum* has the ability to germinate in the dark (Sánchez & Muñoz, 2004), which explains why seedling emergence for this species lasted more time than for the other species during succession (Fig. 3).

4.3 Survival, growth, and reproduction rates after establishment

After seedling recruitment, the three pioneer species reached a peak in population density and then declined at different rates. The lack of seedling recruitment and mortality of juvenile individuals were the main determinants of such decline. High mortality of young individuals is one of the main demographic bottlenecks in the regeneration of pioneer species (Martínez-Ramos et al., 1989), and it is associated both with shade-intolerance and biotic damages caused by natural enemies (e.g pathogens, herbivores; (Dalling & Hubbell, 2002). After reaching a maximum in population density during the first successional year, the mortality rate of *Trema* was over 80% in the small size categories (DBH < 4 cm; Figure 3), and without new recruits compensating this loss, the population strongly declined in

about 90%. *Cecropia* showed a similar trend, which resulted in a decline on population density of 80% after the second year of succession. However, *Cecropia* exhibited a lower mortality rate in small juveniles (< 1 cm DBH) than *Trema* (Figs. 4), coinciding with results from other studies (Brokaw, 1987; Pearson et al., 2003a). This difference explains the presence of juvenile individuals of *Cecropia* and the virtual absence of such individuals of *Trema* after two years of succession (Fig. 2). The lower mortality rates of seedling and juvenile individuals found for *Trichospermum* (Fig. 3) indicate its higher shade tolerance.

Comparative studies have reported that *Trema* and *Cecropia* have higher growth rates than *Trichospermum* (Dalling & Hubbell, 2002; Dalling et al., 2004). Our results, however, show that size-specific RGR were highest for *Trema*, especially in small individuals (DBH < 6 cm), and very similar between *Cecropia* and *Trichospermum* (Fig. 3). The high growth and mortality rates of *Trema* confirm its nature as an early colonizing species. Although *Cecropia* and *Trichospermum* showed similar growth rates, *Cecropia* had higher size-specific mortality and fecundity rates than *Trichospermum* (Fig. 3). Based on the theory of life-history evolution (Silvertown, Franco & Harper, 1999), *Trema* represented an extreme of species with r-strategies (with higher mortality and growth rates), followed in sequence by *Cecropia* and *Trichospermum* (with the lower mortality, growth and fecundity rates).

4.4 Population dynamics

The very low λ values estimated for *Trema* indicated a very fast reduction in population size ($\lambda \ll 1.0$) during the second and third year of succession. This result concurred with the rapid decline of *Trema* after reaching a peak in population density in the first year of succession (Fig. 1). Therefore, the phase of population growth for *Trema* must be restricted

to the first year of succession, at the very beginning of field colonization (see also Pearson et al., 2003a). A similar situation occurred with *Cecropia*, but in this case the rate of population decrease was slower than in *Trema* and the peak of density occurred after one year of succession. In contrast, *Trichospermum* was still increasing after three years of succession ($\lambda > 1$), coinciding with the time at which this species reached its maximum population density (Fig. 1). The lack of estimates of vital rates for all stages of the life cycle for the first two years of succession impeded us to estimate λ in the phase of species' population increase. For pioneer species the latter occurs very fast after field abandonment, as can be inferred from the successional trajectories of change in population density showed in Fig. 1. However, the growth phase may be relatively less important than the decrease phase in determining the period over which a species persist in the successional community. In the three studied species, the rate at which population declined was determined by the permanence probability, especially in the mature stages, which was lower in *Trema*, higher in *Trichospermum* and intermediate in *Cecropia* (Fig. 4). The fact that all elasticity was fully aggregated in such permanence probability is indicative of the relevance of survivorship in mature stages for the long-term dynamics of these species.

Using our estimates for size-specific fecundity rates (Fig.3), we infer that *Cecropia* and *Trichospermum* reached reproductive sizes (DBH > 7 cm) very early in succession (2-3 years after field abandonment; Fig. 2), producing abundant amounts of seeds. However, the recruitment of new seedlings after three years of succession was null in all studied species. This indicates that local seed production does not contribute to population growth. However, the high fecundity of pioneer species, and their wide seed dispersal capacity, plays a key role in the colonization of new disturbed sites (e.g., Álvarez-Buylla, 1994).

Overall, our results support the idea that differences in vital-rates among tropical pioneer tree species represent a regeneration niche (*sensu* Grubb, 1977) partitioning process during succession (Pearson et al., 2003b). *Trichospermum* deviated most in vital rates. Seedlings and juveniles of *Trichospermum* have the ability to recruit, survive and grow even when a forest canopy have been formed and light availability in the understory has decreased (Fig. 3). *Trema* had their regeneration niche requirements as soon as the field was abandoned, followed closely by *Cecropia*. These two species, however, were less differentiated and potentially could compete for site colonization as discussed below.

4.5 Interactions between species during succession

According to the tolerance model of succession proposed by Connell & Slatyer(1977), replacement between species begins with the colonization of several species under an environment rich in resources. Species attaining high population growth rate under such environment are replaced by species with slower population growth rates but with higher competitive ability as resource availability diminishes. This conceptual model apparently fits well with our study system, as suggested by the average successional trajectories of change in population density followed by the studied pioneer species (Fig. 1). However, there was an important variation around these average trajectories, indicating that the species replacement process does not necessarily occurs in a predictable way. For example, in some plots *Trema* attained a high population density while *Cecropia* had very few individuals while the opposite was true in other plots. Apparently, some sort of interference occurred between these species, or a random factors affected the arrival and colonization of the species (*e.g.*, Norden, 2014).

Differences in agricultural land use (Martínez-Ramos et al., 2016) and land use history can lead to different successional trajectories (Williamson, Ganade, Ickes, & Mesquita, 2001; Zermeño-Hernández, Méndez-Toribio, Siebe, Benítez-Malvido, & Martínez-Ramos, 2015). However, our study fields had same agriculture land use (cornfields) and similar land use history (Table S1). Considering that *Trema* and *Cecropia* have similar regeneration requirements, it is possible that an inhibitory priority effect operated on these species. If *Trema* or *Cecropia* first colonize an open site, it will be difficult for the other species to colonize the site and vice versa. In our study system, van Breugel, van Breugel, Jansen, Martínez-Ramos, and Bongers (2012) reported intense competition for light between *Cecropia* and other pioneer species, as was also the case for *Trichospermum*. Other factors affecting seed availability, such as time of field abandonment in the year (as seed production of the species change along the year), year of field abandonment (as seed production of the species may vary in response to interannual climatic conditions; (Fleming & Williams, 1990; Ibarra-Manríquez, G; Sánchez-Garfias B; González-García, 1991), and absence/presence of seed sources nearby to the recently abandoned fields (Arroyo-Rodríguez et al., 2017), might determine what species colonize first a recently abandoned field.

CONCLUSIONS

The studied tree species, although frequently grouped as early pioneer species, were differentiated demographically, exhibiting unsynchronized trajectories of change in population density during the old-field succession in Southern Mexico. *Trema* was the

shortest-lived and most shade-intolerant species, *Trichospermum* the longer-lived and most shade-tolerant one, while *Cecropia* exhibited an intermediate position. The establishment phase was crucial in determining the successional time at which the species reached a peak in population density while survivorship rate in mature stages determined the span of permanence of the species during the successional process. Accordingly, the successional replacement among these pioneer trees could be determined by tolerance mechanisms (Connell & Slatyer, 1977) particularly by the level of shade intolerance of seedlings and juvenile individuals in an environment undergoing a rapid decline in light resources in the forest understorey. However, *Trema* and *Cecropia* exhibited closer regeneration strategies, which could lead to a competitive exclusion process, via priority inhibitory effects, between these species.

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TABLES

Table 1. Land use history of the study plots in Marqués de Comillas, Southern Mexico.

Initial fallow age (years) at the first census, the monitoring interval (year of plot establishment and year of last census), and land use history are shown for each plot. Land use history column: F = fallow age; C = Cornfield; OGF = Old growth forest. Fallow length is indicated in brackets (in years).

Plot	Initial fallow age	Interval of monitoring	Land use history⁺
R-0	0	2004-2014	-
H-0	0	2004-2014	-
R-1	1	2002-2014	F(1)-C-OGF
H-1	1	2000-2014	F(1)-C-F(16)-C-OGF
F-1	1	2000-2009*	F(1)-C-F(16)-C-OGF
P-2	2	2000-2014	F(2)-C-OGF
G-3	3	2000-2014	F(3)-C-OGF
R-4	4	2000-2004*	F(4)-C-OGF
F-4	4	2000-2014	F(4)-C-F(13)-C-OGF
E-4	4	2000-2001*	F(4)-C-OGF
S-8	8	2000-2014	F(8)-C-F(?)-C-OGF
H-10	10	2000-2009*	F(10)-C-OGF
H-17	17	2000-2014	F(17)-C-OGF

* These plots were monitored for a fewer number of years because they were lost due to fires occurred in the vicinity of the plot.

⁺Source: van Breugel et al., 2006

Table 2. Population growth rates for *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum* estimated for two annual successional annual intervals: from the 2nd to the 3rd year, and from the 3rd to the 4th years of succession. Geometric mean lambda (λ) values, its associated standard deviation [SD(λ)] and lower (5%) and upper (95%) percentiles, were obtained generating 1000 lambda values using matrix transition models and a Monte Carlo bootstrapping procedure.

Species	Successional year interval	Λ	SE (λ)	Lower (5%) Percentile	Upper (95%) Percentile
<i>Trema</i>	2-3	0.567	0.004	0.559	0.574
	3-4	0.620	0.003	0.614	0.626
<i>Cecropia</i>	2-3	0.913	0.001	0.911	0.915
	3-4	0.766	0.002	0.763	0.769
<i>Trichospermum</i>	2-3	1.635	0.003	1.632	1.639
	3-4	1.009	0.001	1.008	1.009

LEGENDS FOR FIGURES

Figure 1. Successional trajectories of change in population density of *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum* during the first three decades of old-field succession in Marqués de Comillas, Southern Mexico. Each point represent the mean density for plots sharing same fallow age (vertical lines represent one standard error). Inset are shown scaled trajectories (relative to the maximum population density of each species, taken as 1) drawing by hand.

Figure 2. Successional changes in the population size structure of *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum* during the first three decades of old-field succession in abandoned cornfields in Marqués de Comillas, Southern Mexico. For each year, the percentage of individuals (from the total population) in each of the six size (stage) categories is shown in different hatch patterns.

Figure 3. Size-specific curves of survival, growth, and fecundity rates for *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum* in Marqués de Comillas, Southern Mexico. Inset are shown GLM adjusted models, with the proportion of variance explained (R^2) and associated P values. Based on results of GLM analyses, in each panel, after the species names, the different upper-case letters indicate differences in the origin ordinate and different lower-case letters indicate differences in slope.

Figure 4. Population flux models for *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum* for the second (a) and third (b) year of old-field succession in Marqués de Comillas, Southern Mexico. Ovals represent density of the seed bank and seed

rain. Rectangles indicate density of Seedling (< 50 cm height), Juvenile-1 (50-150 cm height), Juvenile-2 (< 150 cm height and < 1 cm dbh), Juvenile-3 (1-2 cm dbh), Premature (2-4 cm dbh), Mature-1 (4-8 cm dbh), Mature-2 (8-16 cm dbh), and Mature-3 (16-32 cm dbh) stages. Right-headed horizontal or curved arrows are annual progression probabilities (proportion of surviving individuals passing from one to following stage(s)), left-headed dotted curved arrows are annual retrogression probabilities (proportion of living individuals returning to previous stages), circle arrows are annual permanence probabilities (proportion of living individuals remaining in same stage), vertical-down-headed arrows are annual mortality probabilities and vertical-up-headed arrows represent fecundity. Fecundity rates (average number of seeds produced per individual per year) are indicated inside continuous-bordered diamonds above each mature stage. The total number of seeds produced per mature category is indicated inside dotted-bordered diamonds, and the total number of seeds produced by the population per year is indicated inside a thick-bordered diamond. All density values are indicated as individuals per hectare.

Figure 1

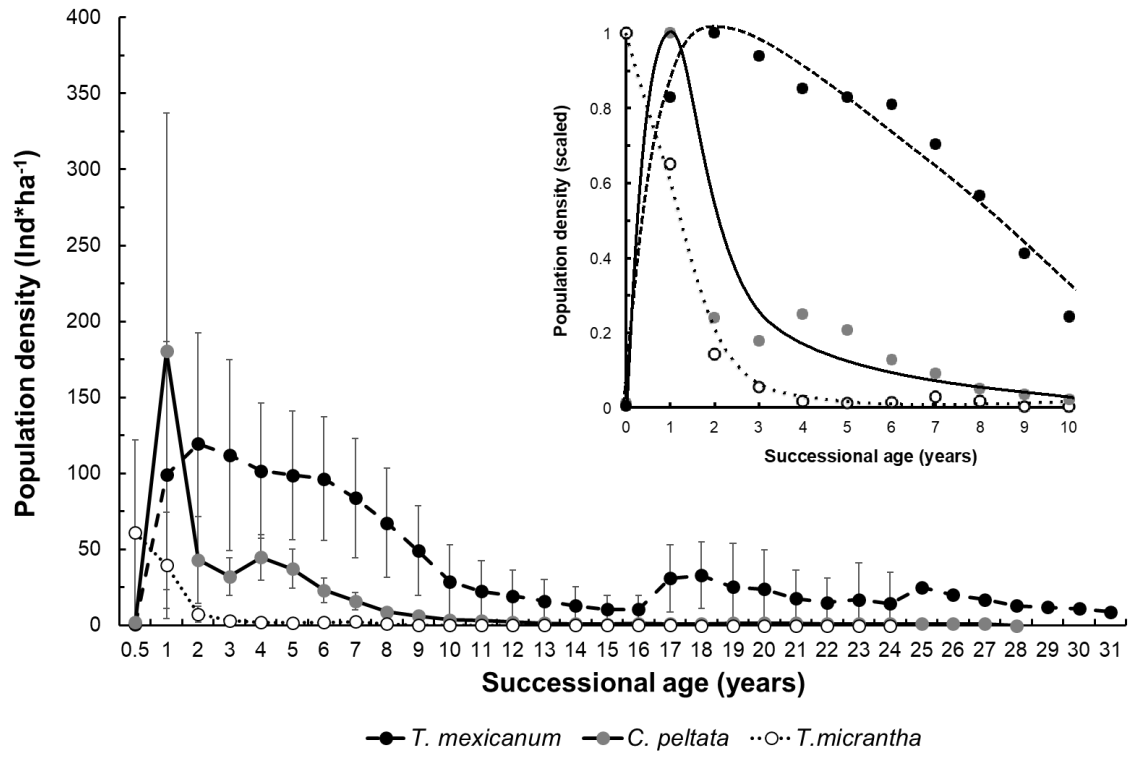


Figure 2

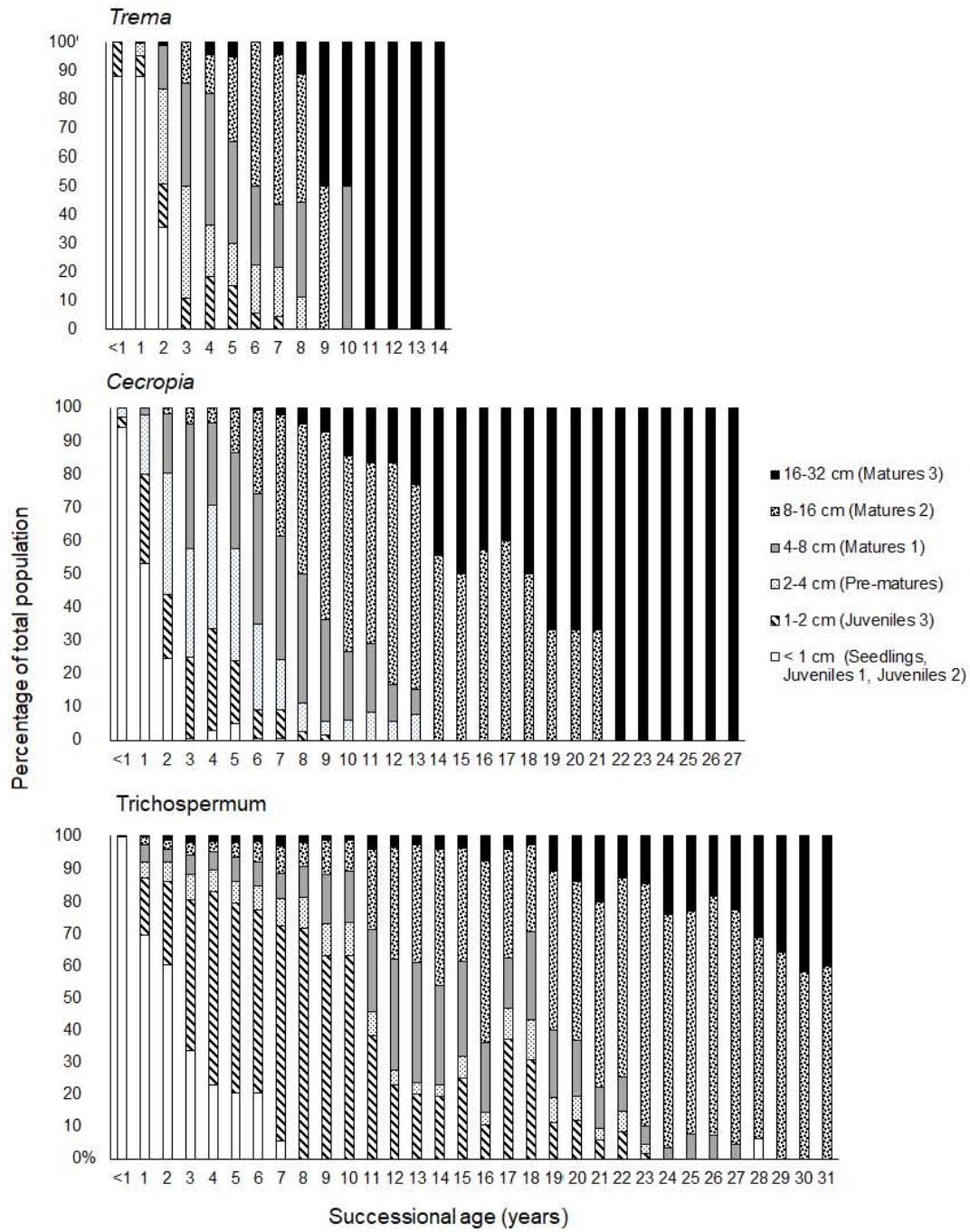


Figure 3

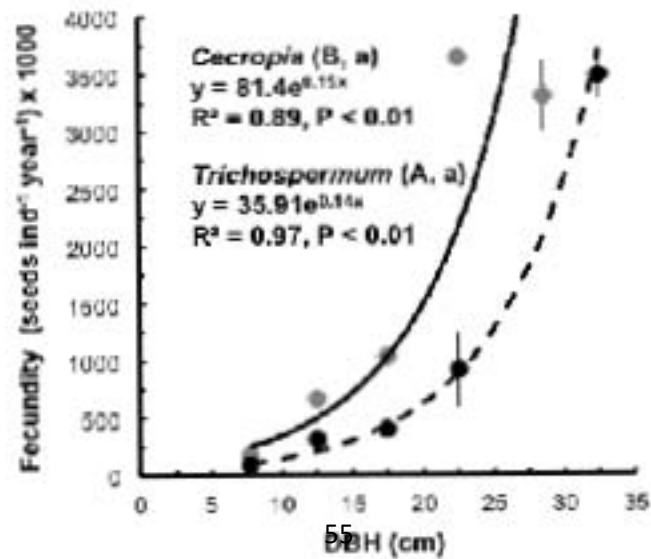
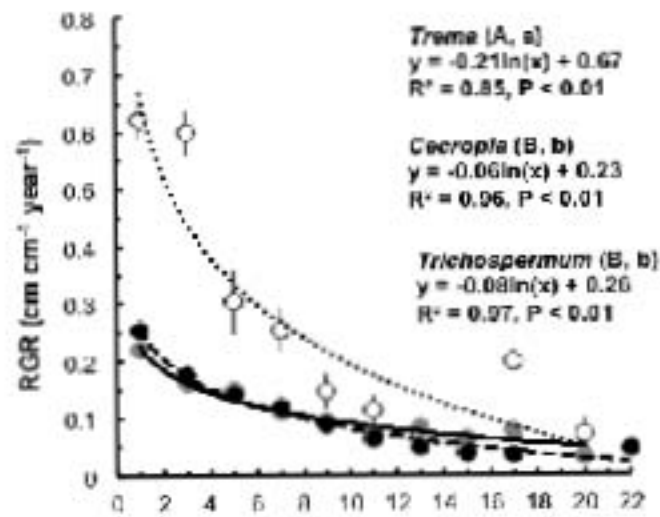
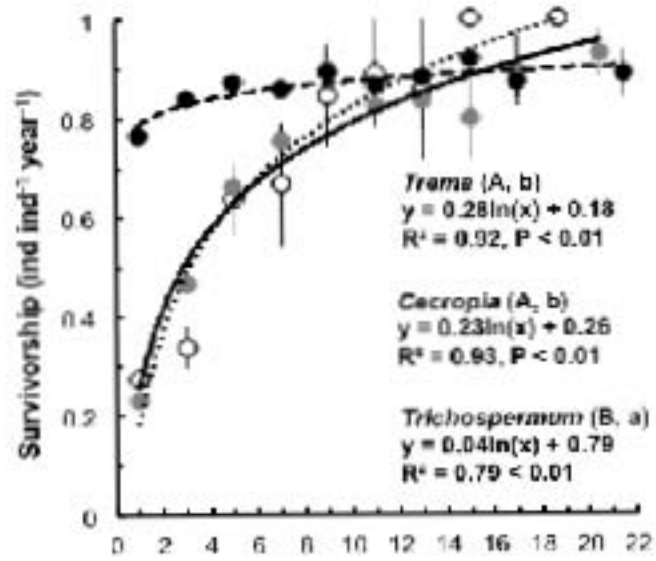
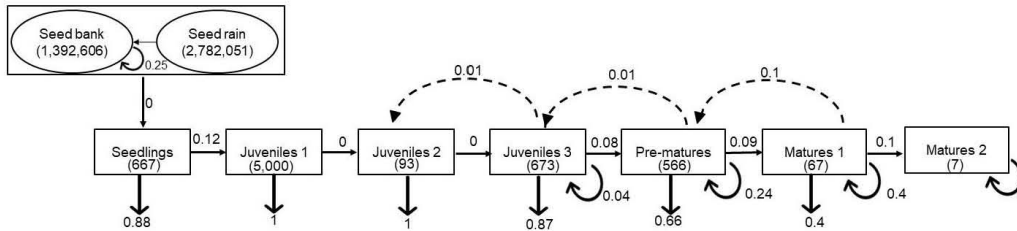


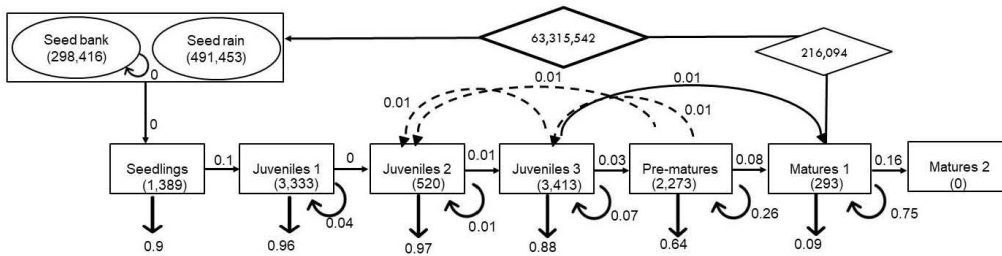
Figure 4

a)

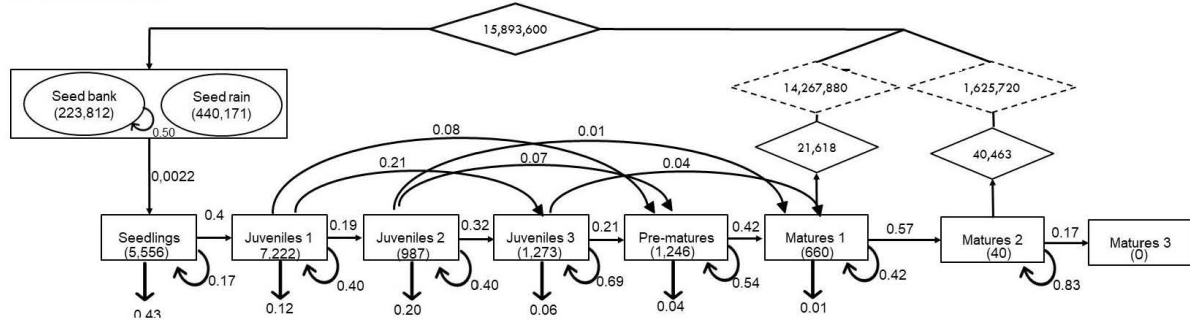
T. micrantha



C. peltata

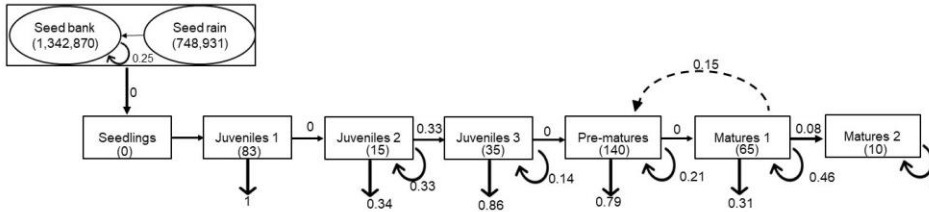


T. mexicanum

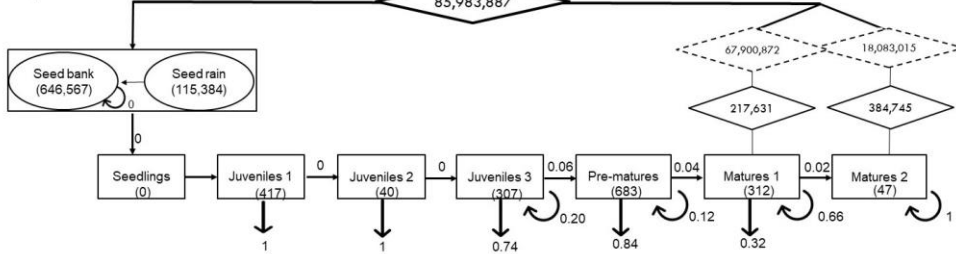


b)

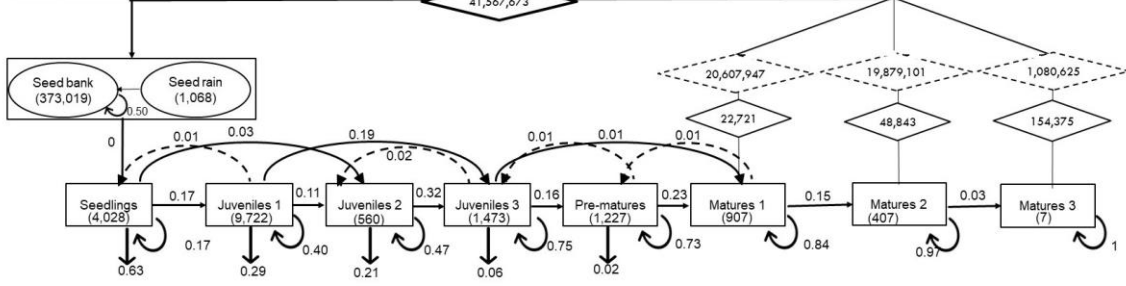
T. micrantha



C. peltata



T. mexicanum



SUPPORTING INFORMATION

Appendix 1: Life history and functional traits of *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum*

Table S1. Reproductive and germination attributes of *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum*.

Species	Seed mass (mg) ¹	Seed dispersal mode ²	Fruiting phenology ^{2,3}	Seed bank ³	Germination type ^{4,5}
<i>Trema</i>	2.8	Zoochory	Masive & continuous	Short-term	Photoblastic
<i>Cecropia</i>	1.0	Zoochory	Masive & continuous	Short-term	Photoblastic
<i>Trichospermum</i>	2.5	Anemochory	Masive discontinuous (dry season)	Long-term	Thermoblastic

Sources

- 1-Lohbeck, 2014
- 2-Ibarra-Manríquez et al., 1991
- 3-Martínez-Ramos et al., 2016
- 4-Pearson et al. 2002
- 5-Sánchez & Muñoz, 2004

Table S2. Functional traits of *Cecropia peltata*, *Trema micrantha* and *Trichospermum mexicanum*. Abbreviation: LS: leaf area (cm²); SLA: specific leaf area (cm g⁻¹); LDW: leaf dry mass content (mg g⁻¹); LT: leaf thickness (mm); WD: wood density (g cm³); SD: stomatal density; N: leaf nitrogen content (mg g⁻¹); P: leaf phosphorus content (mg g⁻¹).

Specie	LA (cm ²)	SLA (cm gr ⁻¹)	LDMC (dry weigth(mg) /fresh weigth (g))	LT (mm)	WD (g cm ⁻³) ³	SD ⁵	N ⁵	P ⁵
<i>Cecropia</i>	2506 ¹	141.1 ¹	381.3 ¹	0.16 ¹	0.24	142	22.08	1.22
<i>Trema</i>	55 ¹	212.6 ¹	285.1 ¹	0.18 ¹	0.28	496	22.93	1.51
<i>Trichospermum</i>	85	166.6 ²	378.1 ²	0.17 ²	0.24	299	18.06	1.11

Sources:

- 1- Lohbeck, 2014

- 2-Tauro, 2013
- 3-Chave et al., 2006
- 4-Brokaw, 1987
- 5-Bongers & Popma, 1990

Appendix 2: Combining chronosequence and dynamic approaches for demographic analyses

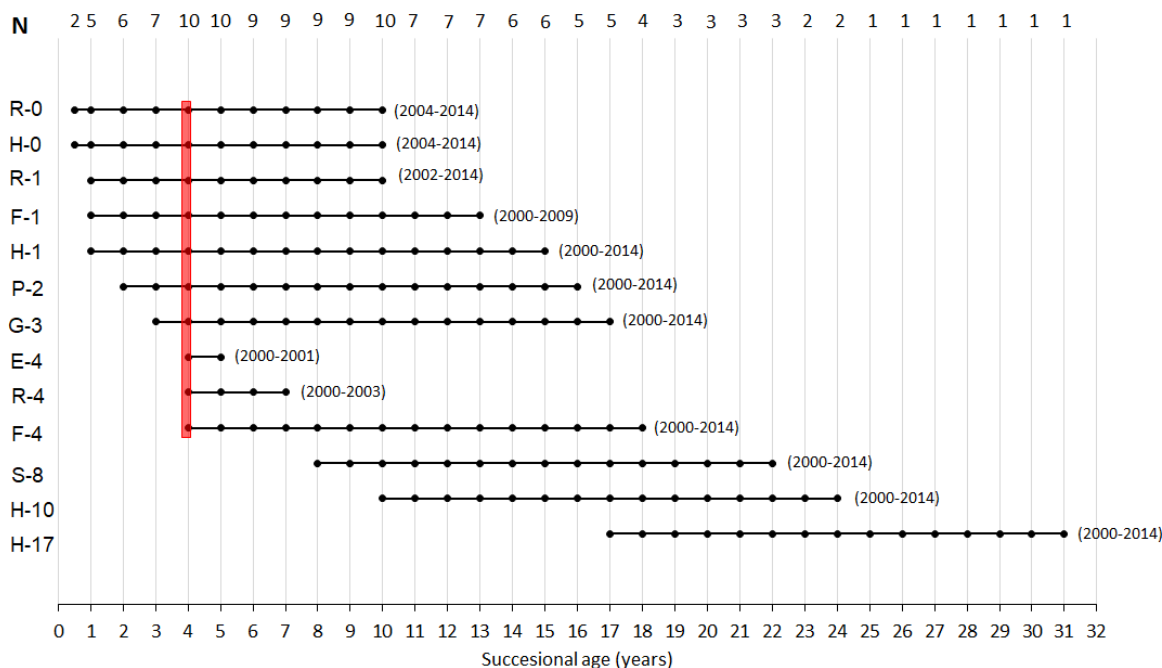
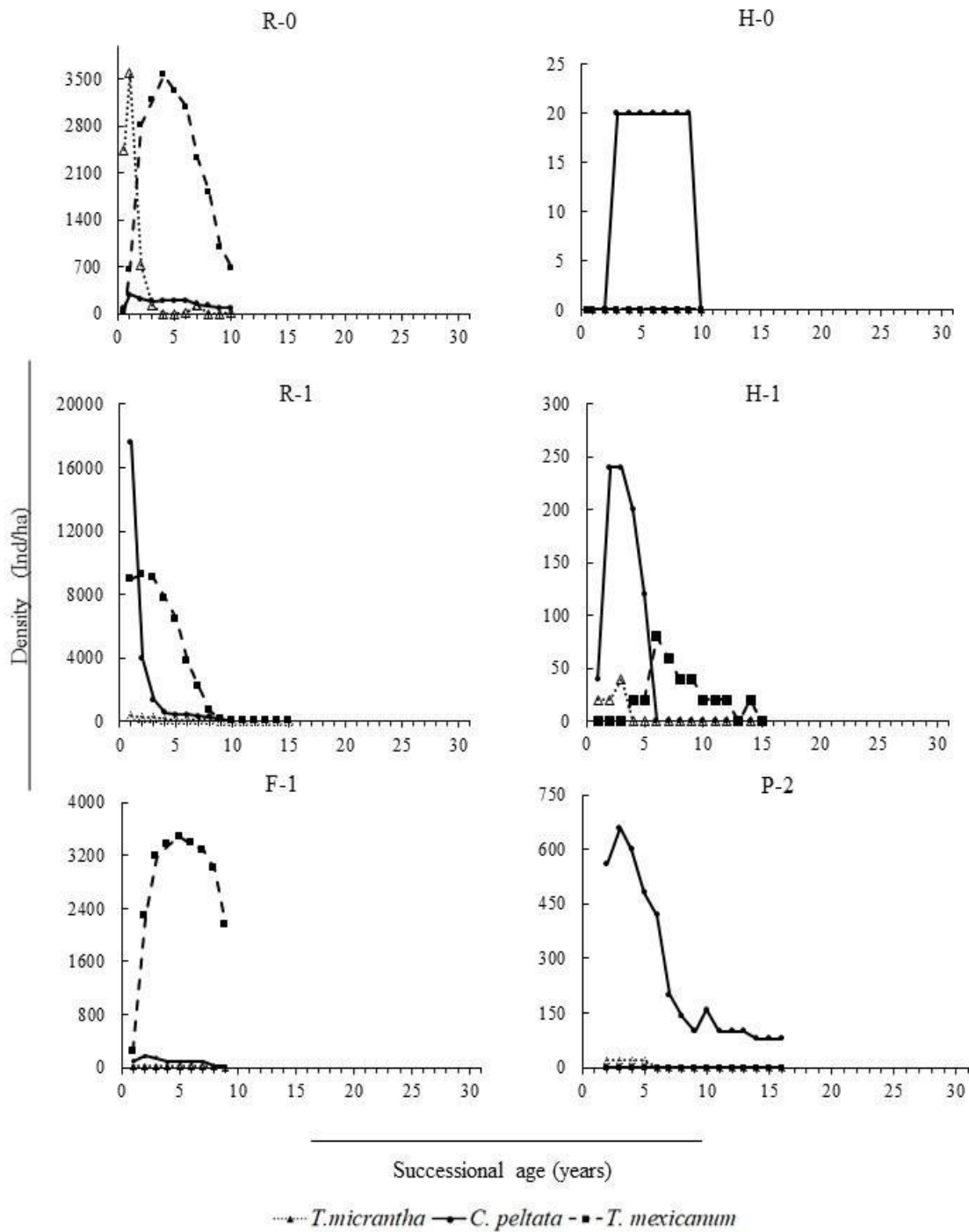


Fig S1: Scheme of the method used in the demographic analyses of studied pioneer species, which combined chronosequence and dynamic approaches. In the x-axis is indicated years after field abandonment. Labels in the left side of figure indicate different permanent plots, the lines indicate the years (dots) of sampling in each plot, and the numbers in brackets the first and the last years of census. The starting dot indicates the fallow age at the first census. Vertical red line exemplify that we used data from different plots with same fallow age for our demographic analyses. For example, population density for the fourth year of succession was calculated as the mean population density based on values from ten plots of that age. In the top of the figure the number of plots for each successional year is shown.

Appendix 3: Successional trajectories in population density of *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum* in each studied plot.



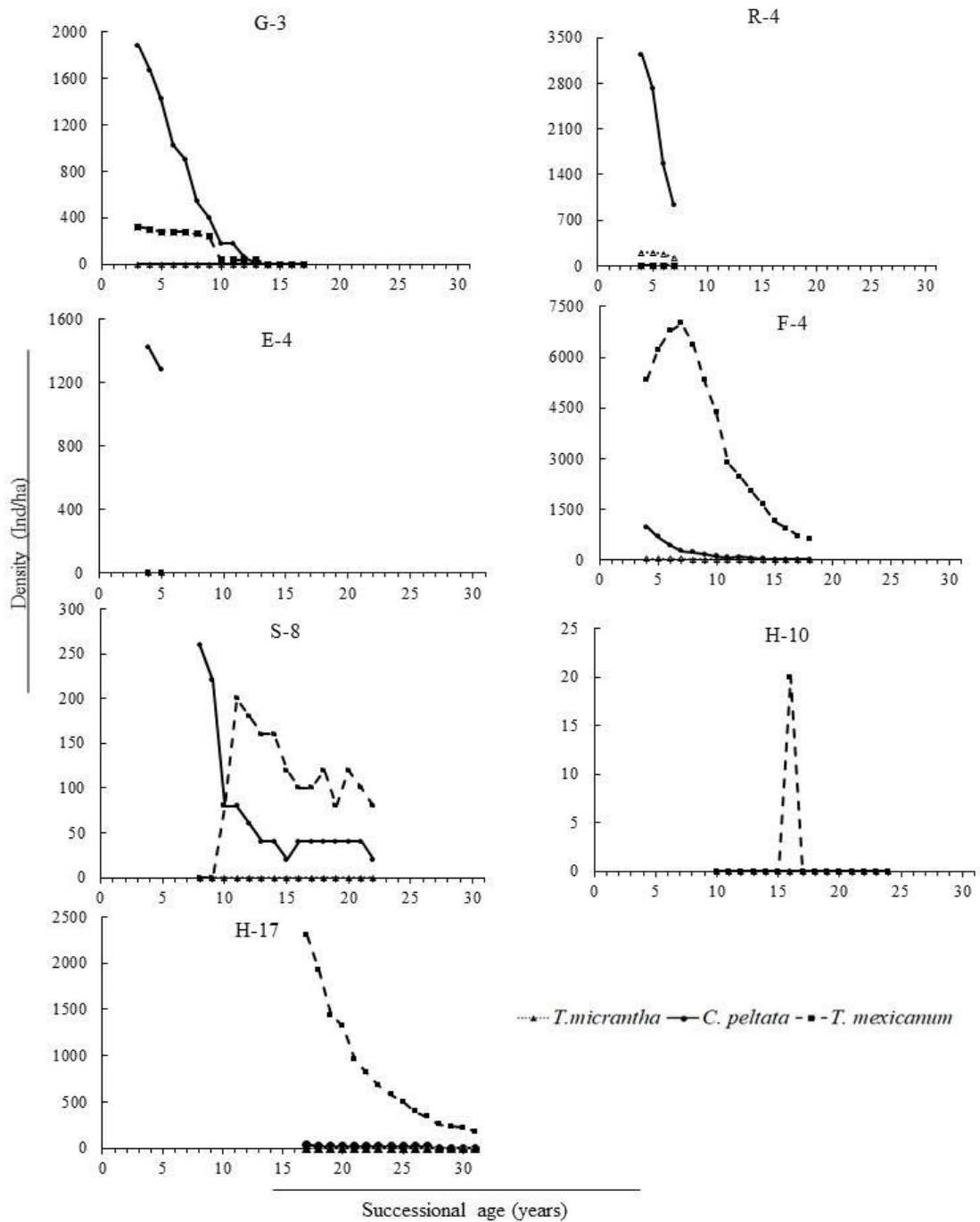


Figure S2. Successional trajectories of population density (ind ha⁻¹) of *Trema micrantha*, *Cecropia peltata* and *Trichospermum mexicanum* in each of 13 plots established in abandoned cornfields in Marqués de Comillas, south-eastern Mexico. The label in the upper-mid part of each graph identifies each plot, with the number indicating the fallow age (years) of the plot at the beginning of the study. Note that the scale of the y-axis varies among plots.

Appendix 4: Description of methods used to estimate fecundity rate as a function of diameter at breast height (DBH) in *Cecropia peltata* and *Trichospermum mexicanum* in secondary forests at Marqués de Comillas, México.

For *C. peltata* and *T. mexicanum*, in July 2017 we selected 24 and 35 individuals potentially reproductive individuals, respectively, covering a size range of 6 to 40 DBH, to estimate size-specific fecundity rates (i.e. seeds production per tree per year). These individuals were located outside our study plots, in patches of secondary forest and along trails. From July 2017 to July 2018, we recorded monthly the reproductive stage (with or without fruits).

For *Cecropia peltata* we counted the number of clusters of spadices per branch, in 38 branches of 10 individuals of different sizes. Then, from 40 clusters, we calculated the mean number of spadices per cluster. We estimated the mean number of seeds per spadix by obtaining the mean length of a spadix (from 16 spadices collected from different individuals), the mean number of seeds in 1-cm length section of the spadices (n = 16) and multiplying the mean total length of a spadix by the mean seeds per 1-cm length section. Then, the equation used to estimate the number of seeds per branch was:

$$\text{Seeds per branch} = (\text{mean number of seeds spadix}^{-1}) \times (\text{mean number of spadices cluster}^1) \times (\text{clusters branch}^{-1})$$

Mean number (\pm s.e.) of clusters per branch was 7.8 ± 0.5 . Mean number of spadices per cluster was 4 ± 0 and the mean number of seeds per spadix was $2,935 \pm 185.7$. With these figures we estimated 93,920 seeds per branch. Each month we recorded the number of branches with clusters in the sampled individuals to have an approximation of the number of seeds produced per tree.

For *Trichospermum mexicanum* we obtained the mean number of bunches with fruits in secondary reproductive branches (n = 44 branches from different individuals). Then, we estimated the mean number of fruits per bunch (n = 57 bunches) and the number of seeds

produced per fruit ($n = 80$ fruits). The equation used to calculate the number of seeds per reproductive branch was:

$$\text{Seeds per branch} = (\text{mean number of seeds fruit}^{-1}) \times (\text{mean number of fruits bunch}^{-1}) \times (\text{mean number of bunches branch}^{-1})$$

The mean (\pm s.e.) number of bunches per branch was 9.5 ± 0.5 ; the mean number of fruits per bunch was 105 ± 8.5 and the mean number of seeds per fruit was 11 ± 0.4 . With values, the estimated mean number of seeds per branch was 10,972.5.

When possible, we recorded monthly, the number of bunches per individual, but in some cases bunch counting was not possible because of visual limitation. In these cases, the number of secondary reproductive branches was used to estimate the number of seeds per individual.

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DISCUSIÓN

Los estudios demográficos en sistemas en proceso de sucesión se han enfocado principalmente en comparar especies que dominan en diferentes momentos (Marcante et al., 2009; Martínez-Ramos et al., 1989; Primack & Lee, 1991), o en analizar los cambios de las tasas vitales de una misma especie en diferentes etapas sucesionales (Otárola & Avalos, 2014; Pascarella et al., 2007; Valverde & Silvertown, 1998). Estos estudios han respaldado la teoría ecológica donde se propone que los cambios en la comunidad a lo largo del tiempo se dan debido a diferencias en las estrategias de historias de vida entre las especies que participan en la sucesión, y que las tasas vitales específicas de cada estado (tamaño, edad) varían dentro de una misma especie dependiendo de la etapa sucesional del sistema. Hasta donde sabemos, este es uno de los primeros trabajos que, a partir de un enfoque demográfico comparativo, muestra que hay variación en la demografía y en la dinámica poblacional entre especies pioneras a lo largo de la sucesión secundaria. La densidad y estructura poblacional cambiaron diferencialmente entre las especies de estudio a lo largo de la sucesión, así como las tasas vitales específicas de cada categoría de tamaño. *Trema* fue la primera colonizadora y de vida corta (<10 años) seguida de *Cecropia* (<28 años), ambas seguidas finalmente por *Trichospermum* (>31 años). Dichas diferencias se relacionaron con el proceso de remplazo entre especies pioneras reportado en estudios previos en las parcelas de estudio (van Breugel et al., 2007). Estos resultados sugieren que la variabilidad demográfica entre especies pioneras permite que, aunque este grupo de

especies compartan algunos rasgos de su historia de vida, cada especie pionera pueda participar en un momento específico de la sucesión.

La posibilidad de que una especie participe en un proceso sucesional depende de diversos factores, que pueden ser tanto estocásticos como determinísticos (Arroyo-Rodríguez et al., 2017; Norden et al., 2015). La limitación en la dispersión, el filtro ambiental para el establecimiento de plántulas, las fluctuaciones temporales en el reclutamiento y diversos factores densodependientes son algunos de los principales procesos ecológicos que determinan la presencia de una especie en un proceso sucesional (Norden, 2014). El remplazo entre especies pioneras en el bosque húmedo tropical puede estar asociado con las diferencias interespecíficas en la forma en que estos factores operan sobre las poblaciones a lo largo de la sucesión (Falinska, 1993; Halpern, 1989b; van Breugel et al., 2007). A pesar de que estas especies comparten algunos aspectos de su historia de vida, algunos estudios han encontrado que las especies pioneras difieren en sus requerimientos para la germinación, el establecimiento de plántulas y los requerimientos de luz para el crecimiento y supervivencia de los individuos. En los siguientes párrafos discutimos cómo algunas de las diferencias en los requerimientos para la regeneración pueden estar relacionadas con los diferentes comportamientos demográficos que encontramos en nuestros resultados para las especies de estudio a lo largo de la sucesión.

Disponibilidad de semillas y limitación de la dispersión

Dos años después de que las parcelas fueron abandonadas, para las especies de estudio se reportó una densidad de semillas muy alta tanto en la lluvia como en el banco de semillas

(Fig. 4-*sobretiro articulo*). En campos agrícolas recién abandonados las semillas presentes pueden venir de árboles cercanos (Finegan, 1984) o del banco de semillas (López-Toledo & Martínez-Ramos, 2011; Quintana-Ascencio, González-Espinosa, Ramírez-Marcial, Dominguez-Vazquez, & Martinez-Ico, 1996). Es bien sabido que las especies de estudio producen abundantes semillas de tamaños pequeños que son dispersadas tanto por animales (*Trema*, *Cecropia*) o por viento (*Trichospermum*) (Alvarez-Buylla & Martínez-Ramos, 1992; Ibarra-Manríquez, G; Sánchez-Garfias B; González-García, 1991; Rodríguez-Velázquez et al., 2009). Teniendo en cuenta esta información y de acuerdo con nuestros resultados, se puede concluir que al momento en que se abandonaron las parcelas de estudio, la disponibilidad de semillas no fue un factor limitante para la colonización de ninguna de las tres especies. Por otro lado, durante el segundo año de sucesión en las tres especies la lluvia de semillas fue por lo menos dos veces mayor que la densidad de semillas reportadas en el banco, pero en el tercer año de sucesión la lluvia de semillas disminuyó en todas las especies y el banco de semillas pasó a ser la fuente de propágulos más importante (Fig. 4-*Sobretiro articulo*). Es necesario realizar otros estudios que permitan analizar si dichas diferencias interanuales respecto a la producción de semillas fueron determinadas por variación climática entre los años de estudio o debido a un incremento en los niveles de competencia inter específica.

Reclutamiento de plántulas y limitación en el establecimiento

Nuestros resultados indican que el periodo óptimo para el reclutamiento de las plántulas una vez iniciado el proceso de sucesión fue muy corto para las tres especies y presentó diferencias entre estas. Para *Trema* este periodo de tiempo estuvo restringido al principio de la sucesión ya que no se reportaron nuevas plántulas en parcelas con más de un año de abandono. *Cecropia* presentó un patrón similar, mientras que para *Trichospermum* se reportaron nuevas plántulas reclutadas en parcelas con más de dos años de sucesión. Este comportamiento en el reclutamiento de plántulas se ha reportado para *Trema* y *Cecropia insignis* (especie del mismo género que *Cecropia peltata*) en procesos de regeneración luego de la apertura de claros en el bosque húmedo de Panamá (Brokaw, 1987). También se ha reportado que para *Cecropia* el periodo óptimo de reclutamiento de plántulas en áreas de borde perturbadas es de dos años luego del disturbio (Fleming & Williams, 1990). Teniendo en cuenta que la germinación de las semillas tanto de *Trema* como *Cecropia* requiere de niveles de luz altos y de fluctuaciones en la temperatura muy marcadas (T. Pearson et al., 2002; Válio & Scarpa, 2001; Vázquez-Yanes & Smith, 1982), es de esperar que el reclutamiento se vea muy limitado una vez se haya formado el dosel en el bosque. Investigaciones realizadas en nuestra zona de estudio han demostrado que la disponibilidad en el sotobosque disminuye rápidamente conforme avanza la sucesión, y en bosques con 10 años de sucesión la radiación fotosintéticamente activa es similar a la reportada en bosques maduros (Ricaño, 2007). Por el contrario, *Trichospermum* tiene la capacidad de germinar en la sombra (Sánchez & Muñoz, 2004), lo cual explica porque el establecimiento

de plántulas para esta especie dura más tiempo durante la sucesión en comparación a las otras especies.

Supervivencia, crecimiento y reproducción después del establecimiento

Después del establecimiento de plántulas las tres especies de estudio alcanzaron su pico de abundancia (con diferencias temporales entre ellas), y luego la densidad poblacional empezó a disminuir (Fig. 1-*Sobretiro articulo*). El patrón de disminución fue diferente entre las especies. Nuestros resultados sugieren que la falta de reclutamiento y tasa de mortalidad de individuos jóvenes es uno de los determinantes principales en el proceso de disminución de las poblaciones. Dos años después de alcanzar su máxima densidad de individuos, las tasas de mortalidad de *Trema* eran mayores a 80% para las categorías de tamaño pequeñas (DAP<4 cm) (Fig. 4-*Sobretiro articulo*), lo que causó una disminución drástica de alrededor del 86% del total de la población en este periodo de tiempo. *Cecropia* mostró un patrón similar, y tasas de mortalidad similares para los individuos jóvenes, lo que resultó en una disminución en la densidad de alrededor del 80% en el segundo año de sucesión; solo un año después de alcanzar su densidad máxima. Sin embargo, la forma en que ocurrió la disminución en los años posteriores fue menos drástica que para *Trema*. A pesar de que ambas especies son intolerantes a la sombra, pero tanto las plántulas como los juveniles de *Trema* presentaron tasas de mortalidad más altas que *Cecropia* bajo condiciones de sombra (Fig. 4-*Sobretiro articulo*), lo cual coincide con los resultados reportados en otros estudios (Brokaw, 1987; T. R. H. Pearson et al., 2003a). Esto explica la presencia de individuos juveniles de *Cecropia* en parcelas con más de 5 años de sucesión, en las cuales no se reportó ningún individuo de esta categoría para *Trema* (Fig. 2-*Sobretiro*

artículo). La mortalidad de individuos juveniles es uno de los mayores filtros ambientales que operan sobre la regeneración de especies pioneras (Martínez-Ramos et al., 1989), y está asociada principalmente con factores como la herbívora y la tolerancia a la sombra. Por otro lado, se ha reportado que en el bosque tropical las tasas altas de mortalidad de plántulas e individuos juveniles, se relacionan positivamente con las tasas de crecimiento, debido a una mayor vulnerabilidad a enemigos naturales (e.j patógenos, herbívoros) (Dalling & Hubbell, 2002). Estudios comparativos han reportado que *Trema* y otras especies del género *Cecropia* presentan tasas de crecimiento mayores en comparación a *Trichospermum* (Dalling & Hubbell, 2002; Dalling et al., 2004) lo que podría explicar las bajas tasas de mortalidad encontradas para esta especie, que le permiten permanecer por más tiempo a lo largo de la sucesión.

Dinámica poblacional

Los bajos valores de λ estimados para *Trema* indican una rápida reducción en el tamaño poblacional durante el segundo y tercer año de sucesión. Este resultado coincide con la rápida disminución de *Trema* luego de alcanzar su pico de abundancia en el primer año de sucesión (Fig. 1-*Sobretiro artículo*). Por lo tanto, se concluye que la fase de crecimiento poblacional para *Trema* estuvo limitada al principio del proceso de la sucesión (menos de un año de abandono de las parcelas). Una situación similar ocurrió con *Cecropia*, pero en este caso el pico de densidad se dio luego de un año de sucesión y la tasa de disminución fue menor que para *Trema*. Solamente para *Trichospermum* la estimación de la tasa de crecimiento fue positiva. Esta especie presentó crecimiento poblacional aún luego de tres

años de sucesión, lo cual coincide con el pico de densidad poblacional observado para esta especie en esta etapa sucesional. La falta de estimaciones de las probabilidades de transición para el ciclo de vida completo para los dos primeros años de sucesión nos impidió estimar λ durante la fase de crecimiento poblacional. Para las especies pioneras esta fase de crecimiento ocurre muy rápidamente, como se puede inferir de las trayectorias de cambio de la densidad poblacional (Fig. 1-Sobretiro articulo). Sin embargo, la fase de crecimiento puede llegar a ser menos importante que la fase de disminución para determinar el periodo durante el cual las especies permanecerán a lo largo del proceso de sucesión secundaria. En las tres especies estudiadas, la tasa a la cual la población disminuyó estuvo determinada por la probabilidad de permanencia, en especial de los individuos adultos, la cual fue menor para *Trema*, mayor en *Trichospermum* e intermedia para *Cecropia* (Fig. 4-Sobretiro articulo). El hecho de que la elasticidad calculada estuviera agregada en las probabilidades de permanencia indica la importancia de la supervivencia de estos estados maduros para la permanencia a largo plazo de estas especies durante la sucesión secundaria.

Al usar los valores estimados de fecundidad en función del tamaño (Fig. 3-Sobretiro articulo), calculamos que los árboles de *Cecropia* y *Trichospermum* alcanzan estados reproductivos en etapas muy tempranas de la sucesión, produciendo cantidades muy abundantes de semillas (Fig. 3 y 4-Sobretiro articulo). Sin embargo, el reclutamiento de nuevas plántulas luego de dos años de sucesión solo ocurrió para *Trichospermum*. Esto muestra que la fecundidad de los individuos reproductivos no contribuye al crecimiento poblacional de las actuales poblaciones sucesionales. Sin embargo, en sistemas dinámicos

como los bosques secundarios, expuestos a disturbios tanto naturales como antropogénicos, la fecundidad es fundamental para producir semillas que serán dispersadas y almacenadas en el banco de semillas, y posteriormente serán fundamentales para el reclutamiento de la población luego de un disturbio.

En términos generales, nuestros resultados soportan la idea de que diferencias en el nicho de regeneración (Grubb, 1977) entre especies pioneras determinan las diferencias en la dinámica poblacional durante la sucesión secundaria (T. R. H. Pearson et al., 2003b). Este planteamiento es claro al comparar *Trichospermum* con las otras dos especies de estudio, porque sus requerimientos de regeneración presentan algunas diferencias que hacen posible una diferenciación temporal evidente en la dinámica poblacional a medida que avanza la sucesión. Sin embargo, las condiciones óptimas para la regeneración de *Trema* se dan justo al inicio de la sucesión, muy similar a lo que ocurre en *Cecropia*. Esta similitud podría indicar que potencialmente estas especies podrían llegar a competir por el espacio de colonización, como se discute a continuación.

Interacción entre especies durante la sucesión

De acuerdo con el modelo de sucesión por tolerancia propuesto por (Connell & Slatyer, 1977), el reemplazamiento entre especies inicia con la colonización simultánea de varias especies en un entorno rico en recursos. Las especies que alcanzan una tasa alta de crecimiento poblacional en dicho entorno son reemplazadas por especies con tasas de crecimiento poblacional más lentas, pero con mayor capacidad competitiva a medida que se reduce la disponibilidad de recursos. Este modelo conceptual aparentemente se ajusta

con nuestro sistema de estudio, como lo sugieren las trayectorias promedio de cambio en la densidad poblacional que observamos para las especies pioneras estudiadas (Fig. 1). Sin embargo, hubo una variación importante en torno a estas trayectorias promedio, lo que indica que el proceso de reemplazamiento de especies no necesariamente ocurre de manera predecible. Por ejemplo, en algunas parcelas *Trema* alcanzó una alta densidad poblacional, mientras que *Cecropia* tenía muy pocos individuos, mientras que lo contrario ocurrió en otras parcelas. Aparentemente, algún tipo de interferencia pudo haber ocurrido entre estas especies.

Las diferencias en el uso de la tierra para agricultura (Martínez-Ramos et al., 2016) y la historia de uso pueden conducir a diferentes trayectorias sucesionales (Williamson et al., 2001; Zermeño-Hernández et al., 2015). Sin embargo, nuestras parcelas de estudio tenían el mismo uso de la tierra agrícola (Milpa) y un historial de uso de la tierra similar (Tabla 1- *Sobretiro articulo*). Teniendo en cuenta que *Trema* y *Cecropia* tienen requisitos de regeneración similares, es posible que haya un efecto de prioridad inhibitoria en estas especies. Si *Trema* o *Cecropia* colonizan primero un sitio abierto, será difícil para la otra especie colonizar este sitio y viceversa. En nuestro sistema de estudio (van Breugel et al., 2012) reportaron una intensa competencia por la luz entre *Cecropia* y otras especies pioneras, como también fue el caso de *Trichospermum*. Otros factores que afectan la disponibilidad de semillas, como el momento en el año en que se abandonó el campo (a medida que la producción de semillas de la especie cambia a lo largo del año), el año de abandono de campo (ya que la producción de semillas de la especie puede variar en respuesta a las condiciones climáticas interanuales (Fleming & Williams, 1990; Ibarra-

Manríquez, G; Sánchez-Garfias B; González-García, 1991) , y cercanía a fuentes de semillas cercanas a los campos recientemente abandonados (Arroyo-Rodríguez et al., 2017), podrían determinar qué especies colonizan primero y de esta forma inician el proceso de sucesión secundaria en estas parcelas.

CONCLUSIONES

Las especies arbóreas estudiadas, aunque con frecuencia agrupadas como especies pioneras tempranas, se diferenciaron demográficamente, exhibiendo trayectorias no sincronizadas de cambio en la densidad poblacional durante la sucesión en campos agrícolas abandonados en el sur de México. *Trema* fue la especie de vida más corta e intolerante a la sombra, *Trichospermum* la más longeva y tolerante a la sombra, mientras que *Cecropia* exhibió una posición intermedia. La fase de establecimiento fue crucial para determinar el momento de la sucesión en el que las especies alcanzaron un pico en la densidad poblacional, mientras que la tasa de supervivencia en etapas juveniles y maduras determinó el período de permanencia de las especies durante el proceso de sucesión. En consecuencia, el reemplazamiento sucesional entre estos árboles pioneros podría determinarse mediante mecanismos de tolerancia (Connell y Slatyer, 1977), particularmente por el nivel o intolerancia a la sombra de las plántulas y los individuos juveniles en un entorno que experimenta una disminución rápida de los recursos como la luz, según lo documentado por Ricaño (2007) en nuestro sistema de estudio. Sin embargo, *Trema* y *Cecropia* exhibieron estrategias de regeneración más cercanas, lo que podría conducir a un proceso de exclusión competitiva, a través de efectos inhibitorios prioritarios, entre estas especies.

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