



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

**CAMBIOS TEMPORALES Y ESPACIALES EN LA ESTRUCTURA Y DIVERSIDAD DE LA VEGETACIÓN Y EN
LOS ALMACENES DE CARBONO DE BOSQUES TROPICALES SECOS SECUNDARIOS EN LA REGIÓN DE
CHAMELA, JALISCO**

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

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MÉXICO, DF, JULIO DE 2015



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Dr. Isidro Ávila Martínez
Director General de Administración Escolar, UNAM
Presente.-

Por medio de la presente, me permito informar a usted, que en reunión ordinaria del Subcomité por Campo de Conocimiento (Biología Evolutiva y Sistemática) del Posgrado en Ciencias Biológicas, se aprobó el siguiente jurado para el examen de grado de **Doctor en Ciencias** del alumno **Francisco Mora Ardila** con número de cuenta **505451024** con la tesis titulada: **"Cambios temporales y espaciales de la estructura y diversidad de la vegetación y en los almacenes de carbono de bosques tropicales secos secundarios en la región de Chamela, Jalisco"** bajo la dirección de la **Dra. Patricia Balvanera Levy**, Tutora Principal.-

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Sin otro particular, quedo de usted.

Atentamente
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, D.F., a 15 de junio de 2015



Dra. María del Coro Arizmendi Arriaga
Coordinadora del Programa



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Tres espacios tiene mi corazón,
en su compañía recorreré el camino de la vida.

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Resumen

Los bosques tropicales secundarios, aquellos que resultan de la regeneración natural de la cobertura vegetal boscosa en áreas que fueron impactadas por perturbaciones, se han convertido en un componente dominante de los paisajes tropicales alterados por actividades humanas. En la actualidad se reconoce su importancia, tanto para el mantenimiento de la diversidad biológica en paisajes transformados, como para la provisión de beneficios en general para la humanidad. Se ha planteado que los bosques secundarios desempeñan un papel importante en la mitigación del cambio climático a través del secuestro de carbono. La evidencia científica confirma que los bosques secundarios acumulan carbono, principalmente en su biomasa, a medida que recuperan su estructura, diversidad y funciones a través de la sucesión. Sin embargo, existe aún gran incertidumbre respecto a la naturaleza de estos patrones tanto a lo largo del tiempo como en el espacio. En la presente tesis estudié la recuperación de la estructura, diversidad y almacenes de carbono (C) en un paisaje de bosque tropical seco (BTS) transformado por actividades humanas, evaluando la capacidad explicativa y predictiva de la edad del bosque, la historia de uso y las condiciones biofísicas sobre la recuperación, así como las implicaciones de las relaciones entre dichos atributos de los bosques secundarios para la implementación de estrategias de mitigación del cambio climático (programa REDD+).

La tesis se compone de cinco capítulos. El Capítulo 1 es una introducción general en la que presento el problema de estudio. En ella identifiqué los factores que determinan los cambios espaciales y temporales en la estructura y diversidad de la comunidad vegetal y en los almacenes de C asociados a la sucesión secundaria en los bosques tropicales. Reviso el estado del conocimiento en torno al tema de estudio en el contexto de las regiones estacionalmente secas, con el fin de resaltar los vacíos de información específicos que esta tesis pretendió cubrir y así plantear los objetivos particulares del trabajo. También se hace una breve descripción del sistema de estudio.

En el Capítulo 2 analizo los cambios en la estructura, la diversidad y la composición florística de la comunidad de árboles a través de la sucesión secundaria. Para lograrlo, combiné aproximaciones de cronosecuencia (estática) y de medidas repetidas a través del tiempo (dinámica). Desarrollé una aproximación analítica para comparar la dinámica observada en los sitios con las predicciones generadas a partir de la cronosecuencia. La edad del bosque se relaciona fuertemente con los tres tipos de atributos. Sin embargo, la cronosecuencia muestra en general una baja capacidad predictiva de las tasas de cambio de los atributos analizados, tendiendo a sobreestimarlas. Las variables de sitio asociadas a la historia de manejo explicaron parcialmente la variación en las tasas de cambio. En su conjunto, los resultados indican que la aproximación de cronosecuencia tiene una baja capacidad predictiva sobre cambios de corto plazo, lo que implica la necesidad de usarlas

con precaución en la predicción de la recuperación de servicios ecosistémicos a través de la sucesión.

En el Capítulo 3 evalué la recuperación de los almacenes de C a través de la sucesión secundaria. Para ello, cuantifico los almacenes de C en cuatro compartimentos del ecosistema: en la biomasa aérea viva, en la biomasa de raíces, en el mantillo y en los primeros 10 cm de suelo. Evalué sus cambios a lo largo de la sucesión empleando la cronosecuencia, así como los cambios de corto plazo en la biomasa aérea viva empleando una aproximación dinámica, poniendo a prueba la relación de los cambios de corto plazo con la edad del bosque, el almacén inicial y la diversidad de árboles (taxonómica y funcional) mediante el uso de modelos de ecuaciones estructurales. Se encuentra que los almacenes de C en la biomasa aérea viva de árboles, en el mantillo y en raíces pequeñas se recuperan de manera integrada a través de la sucesión, mientras que las raíces gruesas y el carbono en el suelo no muestran asociación con el tiempo ni con otros almacenes. La edad del bosque y la altura máxima alcanzable por cada especie explican los almacenes de C aéreos, y determinan parcialmente las tasas de acumulación de C. No se encuentra evidencia de un efecto de la diversidad taxonómica. Los resultados del estudio demuestran que los atributos funcionales de la vegetación pueden jugar un papel importante en la recuperación de los almacenes de C a través de la sucesión y sugieren que las tasas de acumulación de C en la biomasa se encuentran altamente sobreestimadas a partir de los modelos de cronosecuencia.

En el Capítulo 4 analizo la asociación a través del paisaje de los almacenes de C en la biomasa aérea y de la diversidad de árboles, evaluando el efecto de factores biofísicos y de manejo en dicha asociación, a escala tanto de sitio como de paisaje. Se encuentra una asociación significativa entre los almacenes de C y la diversidad o la composición florística. Dicha asociación está determinada fundamentalmente por la edad de los bosques, aunque se encuentra mediada también por la historia de uso y la configuración del paisaje. En general, dado un mismo almacén de C, los sitios con menor intensidad de uso y menor preponderancia de la actividad agrícola en el paisaje presentan mayores valores de riqueza y composiciones de especies más similares a las de los bosques no desmontados. A escala del paisaje, las reducciones en el almacén de C son mayores cuando la deforestación se concentra en los bosques maduros, mientras que los mayores cambios en la riqueza y composición de especies ocurren cuando la deforestación se concentra en los bosques sucesionales jóvenes. Los resultados sugieren que, en la selección de áreas para la implementación de REDD+, las oportunidades para maximizar almacenes de C y diversidad se darán en bosques maduros o bosques secundarios avanzados. Se sugieren diferentes estrategias de manejo de los sitios y del paisaje que permitan incluir otras áreas en REDD+, de tal forma que se fomente tanto la recuperación de los almacenes como el mantenimiento de la diversidad.

En el Capítulo 5 presento una discusión general sobre el avance del conocimiento científico aportado por esta tesis en torno a tres aspectos relacionados a la recuperación de los bosques tropicales y los almacenes de C a través de la sucesión secundaria. Discuto en primer lugar la necesidad de la integración de las aproximaciones de cronosecuencia y dinámica para el entendimiento de dicha recuperación, así como las implicaciones para la generación de proyecciones. Posteriormente, resumo la evidencia en torno a la recuperación de la estructura, la diversidad y los almacenes de C a través de la sucesión en el bosque tropical seco de la región de Chamela-Cuixmala, discutiendo al efecto de los factores ambientales y de la historia de uso sobre los almacenes de C y su acumulación a través de la sucesión y proponiendo las implicaciones de dichos resultados para la estimación del papel del bosque tropical seco en el ciclo del C. Por último, discuto las implicaciones de la relación entre diversidad y almacenes de C en el contexto de la implementación del programa REDD+.

Abstract

Tropical secondary forests, those growing from natural regeneration of forest vegetation in areas previously impacted by disturbances, have become a key component of tropical landscapes transformed by human activities. Today its importance for both the maintenance of biodiversity in transformed landscapes, as for the provision of benefits for humanity is recognized. It has been suggested that secondary forests play an important role in mitigating climate change through carbon sequestration. Scientific evidence confirms that secondary forests accumulate carbon, mainly in their biomass, as they recover their structure, diversity and functions through succession. However, there is still much uncertainty about the nature of these patterns along both time and space. In this thesis I studied the recovery of the structure, diversity and carbon (C) stocks in a landscape of tropical dry forest (TDF) transformed by human activities, evaluating the explanatory and predictive capacity of forest age, land use history and biophysical conditions in this recovery, and the implications of their relationships for the implementation of strategies to mitigate climate change (REDD+ program).

The thesis consists of five chapters. Chapter 1 is a general introduction in which I present the aim of the study. The factors that determine the spatial and temporal changes in the structure and diversity of the woody plant community and C stocks associated with secondary succession in tropical forest are identified. I review the state of knowledge on this subject in the context of seasonally dry regions, in order to highlight specific information gaps that this thesis attempted to cover and so raise its particular objectives. The study system is also briefly introduced.

In Chapter 2 I analyze the changes in the structure, diversity and species composition of the tree community along secondary succession. To achieve this, I combined chronosequence (static) and repeated measures over time (dynamic) approaches. I develop an analytical approach to compare the dynamics observed at sites with predictions generated from the chronosequence. Forest age is strongly associated with all three kinds of attributes. However, the chronosequence shows low predictive ability on the attributes' rates of change, with a bias to overestimate them. Variables associated with site management history partially explain the variation in rates of change. Taken together, the results indicate that the chronosequence approach has a low predictive ability on short-term changes, which implies the need to use them with caution when predicting recovery of ecosystem services along succession.

In Chapter 3 I evaluate the recovery of C stocks along secondary succession. I quantify C stocks in four ecosystem compartments: aboveground living biomass, root biomass, surface litter and carbon in the top 10 cm of soil. I evaluate their changes along

succession using the chronosequence, as well as short-term changes in aboveground living biomass of trees using a dynamic approach, testing the relationship between short-term changes in aboveground living biomass and forest age, initial stock and diversity of trees (taxonomic and functional) using structural equation modeling. It is found that C stores in A, surface litter and small roots recover in an integrated manner through the succession, while thick roots and soil carbon showed no association with time or with other stocks. Forest age and the maximum height attainable by each species account for aboveground living biomass in trees, defining partially the short term changes in aboveground living biomass of trees. We found no evidence of an effect of taxonomic diversity. The results show that functional traits can play an important role in the recovery of carbon pools during succession, and suggest that rates of C capture are highly overestimated from chronosequence models.

In Chapter 4 I analyze the association between C in the aboveground biomass, species richness and community composition through space, at both site and landscape levels, and testing the effects of biophysical factors and land management on such association. At site level, a significant relationship between C stock and species diversity and species composition is found. Such association is mainly driven by forest age, although it is also mediated by site use history and landscape configuration. Overall, given the same C stock, sites that were used less intensively or surrounded by a buffer with less proportion of agricultural land have higher species richness and higher similarity to old growth forests. At the landscape level, reductions in C stock are largest when deforestation concentrated on old growth forests, while the largest reduction in species richness and a more profound modification in species composition arose when concentrated on young secondary forests. Our results suggest that, while targeting areas for REDD+ implementation, the opportunity to maximize both C stocks and biodiversity are highest in sites and landscapes with a higher proportion of non-previously deforested land or forests older than thirty years. Other areas could be targeted for REDD+ if alternative management activities beyond conservation are implemented, aimed at increasing C stocks or biodiversity.

In Chapter 5 I present a general discussion on how the scientific knowledge on secondary succession and the recovery of carbon stocks in tropical dry forests advanced with this thesis. First I discuss the need for integrating chronosequence and dynamic approaches to achieve a better understanding of the recovery through succession, particularly for estimating the role tropical secondary forests could play in climate change mitigation. Then I discuss the relevance of environment, diversity and land use history as drivers of the recovery of forest structure, diversity, and C stocks along succession in the tropical dry forest of the Chamela-Cuixmala region. Finally, I discuss the implications of the findings reported in this thesis for the implementation of REDD+ towards both carbon stocks and biodiversity conservation in the dry tropics.

Capítulo 1. *Introducción general*

Francisco Mora

Bosques tropicales y cambio global

El cambio de uso y cobertura del suelo (CUCS) constituye uno de los principales procesos asociados al cambio global. En el último siglo, los bosques tropicales han sufrido transformaciones profundas asociadas a dicho proceso (Wright, 2005, 2010; Miles *et al.*, 2006) y se estima que más de 60 % de los bosques tropicales existentes en la actualidad presentan evidencia de algún tipo de acción humana directa (FAO, 2009). De manera general, es posible clasificar las transformaciones causadas por el CUCS de acuerdo con sus efectos sobre la estructura del bosque en dos grandes categorías: deforestación y degradación (Ver Recuadro 1.1.). La deforestación ha sido principalmente resultado de la expansión de la frontera agropecuaria, aunque la extracción de madera y la expansión de infraestructura (principalmente la construcción de carreteras y el crecimiento de las áreas urbanas) constituyen también inductores importantes de la deforestación (Geist y Lambin, 2002; Sánchez-Azofeifa y Portillo-Quintero, 2011). La degradación es causada principalmente por la tala selectiva, la extracción de leña, el pastoreo y el fuego (DeFries *et al.*, 2007). Estas causas no son mutuamente excluyentes, de tal forma que la deforestación puede estar asociada a un proceso de degradación previo (Figura 1.1.). Dichos disturbios modifican total o parcialmente la estructura de la vegetación (Wright, 2010; Berenguer *et al.*, 2014), la diversidad y la composición de especies (Wright *et al.*, 2006; Gibson *et al.*, 2011), y las funciones del ecosistema (Bruijnzeel, 2004; García-Oliva y Jaramillo, 2011), con consecuencias importantes sobre la capacidad de estas áreas de brindar beneficios a la humanidad (Foley *et al.*, 2007).

La dinámica de transformación humana de los bosques tropicales incluye también el abandono de áreas usadas previamente para actividades agropecuarias (Figura 1.1). En dichas áreas comúnmente tiene lugar un proceso de sucesión secundaria (Recuadro 1.1), a través del cual el bosque recupera sus atributos estructurales, su diversidad y sus funciones (Guariguata y Ostertag, 2001; Chazdon, 2008; Quesada *et al.*, 2009). Los bosques secundarios abarcan entre 2 y 25 % de los bosques tropicales en diferentes regiones del mundo (Helmer, 2000; Foley *et al.*, 2007; Wright, 2010). Debido a su representatividad actual y la preponderancia esperada en las próximas décadas a través de los paisajes tropicales (Chazdon, 2014), entender cómo cambia su estructura y funcionamiento a través del espacio y el tiempo constituye un tema de prioridad para la investigación científica (Chazdon *et al.*, 2009a; Quesada *et al.*, 2009), dada su relación con otras dimensiones del cambio global, tales como la pérdida de la diversidad biológica o el cambio climático.

Recuadro 1.1. Glosario de términos usados en esta investigación.

Abandono de parcela agropecuaria: cese de las actividades de manejo asociadas con el mantenimiento de los potreros para la producción pecuaria. El manejo de un potrero implica comúnmente el corte de la vegetación leñosa, la aplicación de herbicidas, el uso de fuego o la dispersión de semillas de pastos (Burgos & Maass, 2004; Trilleras *et al.*, 2015). El abandono no implica sin embargo el cese de actividades extractivas y/o productivas, entre las que se encuentran el ingreso del ganado y la extracción de productos forestales (Cohen, 2014).

Almacén de carbono: cantidad de carbono almacenado en un compartimento particular de un ecosistema (Chapin III *et al.*, 2011).

Bosque tropical seco (BTS): formación boscosa que se desarrolla en regiones con un promedio de temperatura anual superior a 17°C, con precipitación entre 250 y 2000 mm/año y con un claro régimen estacional, en el que la precipitación es inferior a 100mm/mes durante al menos cuatro meses. Esta sequía estacional determina la pérdida casi total del follaje durante la estación seca (Dirzo *et al.*, 2011).

Bosque maduro (old growth o mature forests en inglés): bosques cuya estructura, composición y funcionamiento son relativamente estables (Chazdon, 2014) y responden principalmente a los condicionantes regionales y locales, tales como el clima o el suelo. En términos prácticos, corresponden a áreas para las que no existe registro o evidencia de disturbios recientes que hayan modificado su estructura y funcionamiento significativamente (Putz & Redford, 2010).

Bosque secundario: bosques que se originan por el recrecimiento de la vegetación en áreas cuya cubierta boscosa original fue modificada de manera significativa por la acción de un disturbio (Chokkalingam & De Jong, 2001). En este trabajo se empleará el término para hacer referencia particular a áreas deforestadas para el desarrollo de actividades agropecuarias (Guariguata & Ostertag, 2001; Putz & Redford, 2010).

Captura de carbono: acumulación neta de carbono de origen atmosférico (CO₂) en un ecosistema como resultado del balance entre el carbono fijado a través del proceso de fotosíntesis (*captura sensu stricto*) y las pérdidas de carbono en el ecosistema causadas por procesos naturales (ej. respiración, lixiviación) o de origen humano (ej. Fuego, pastoreo).

Cronosecuencia: Aproximación para el estudio de la sucesión en el que se comparan sitios con diferente tiempo transcurrido desde que cesó el disturbio para inferir patrones de cambio a través de la misma (Walker *et al.*, 2010).

Deforestación: cambio de cobertura del suelo de forestal a no forestal (inferior a 30% de cobertura del dosel) como resultado de las actividades humanas (IPCC, 2006).

Degradación: pérdida parcial de atributos estructurales (cobertura, área basal) sin rebasar el límite definido para deforestación (IPCC, 2003).

Bosques tropicales y el ciclo del carbono

Los bosques tropicales son un componente clave del ciclo global del C. Su relevancia se debe a que constituyen el mayor almacén de C en la vegetación a nivel mundial (Houghton *et al.*, 2009; Chapin III *et al.*, 2011), asociado a su extensión, su alta productividad y la capacidad de almacenamiento potencial (Keith *et al.*, 2009; FAO, 2010; Donato *et al.*, 2011; Grace *et al.*, 2014). También constituyen un agente fundamental en el proceso de cambio climático global. Síntesis recientes muestran que la deforestación y la degradación de bosques tropicales son las responsables de la emisión a la atmósfera de aproximadamente 1.2 Pg C al año, lo que representa alrededor de 12 % de las emisiones totales de gases de efecto invernadero (GEI) durante las últimas dos décadas (van der Werf *et al.*, 2009; Houghton *et al.*, 2012; Grace *et al.*, 2014). Sin embargo, se presenta un alto nivel de incertidumbre en dichas estimaciones, así como en el aporte relativo de diferentes tipos de bosques tropicales al almacenamiento de C y a las emisiones de GEI globales (Houghton *et al.*, 2009; Achard *et al.*, 2014). En particular, para el caso del bosque tropical seco (BTS), las escasas estimaciones disponibles proponen emisiones de 0.14 a 0.33 Pg C al año, lo que representa entre 15 y 38 % de todas las emisiones tropicales por deforestación (Harris *et al.*, 2012; Achard *et al.*, 2014). Este aporte reducido del BTS está asociado a sus menores tasas de deforestación (Mayaux *et al.*, 2005; Hansen *et al.*, 2010; Harris *et al.*, 2012; Achard *et al.*, 2014) y a la menor densidad de C en el BTS (Achard, 2004; IPCC, 2006).

Pero los bosques tropicales actúan no sólo como emisores de C a la atmósfera como resultado de su deforestación o degradación, sino también como sumideros temporales o permanentes. El monitoreo a largo plazo de parcelas permanentes ha permitido confirmar un incremento en la biomasa aérea de bosques maduros, aunque la magnitud total de la captura de C asociada presenta un alto nivel de incertidumbre: 0.5-1.3 Pg C/año, de los que entre 25 y 38 % ocurre en el BTS (Lewis *et al.*, 2009; Malhi, 2010; Pan *et al.*, 2011; Grace *et al.*, 2014) y estudios recientes muestran una reducción a largo plazo de la biomasa aérea en regiones como la Amazonía (Brienen *et al.*, 2015). Sin embargo, la mayor parte de la captura de C en las regiones tropicales ocurre en los bosques secundarios o degradados. Se estima que dichos bosques han capturado en su biomasa aérea entre 0.1-1.6 Pg C año⁻¹ en las últimas dos décadas (Pan *et al.*, 2011; Baccini *et al.*, 2012; Harris *et al.*, 2012; Achard *et al.*, 2014; Grace *et al.*, 2014), aunque como se observa, hay mucha incertidumbre al respecto, asociada tanto a la estimación de la extensión de los bosques secundarios, como a su potencial de captura de C (Defries *et al.*, 2002; Cleveland *et al.*, 2011), poniendo en evidencia la necesidad de desarrollar estudios que permitan entender las causas de la variación en las tasas de captura de C en estos bosques.

Sucesión ecológica en áreas agropecuarias abandonadas

El proceso de sucesión secundaria en áreas agropecuarias abandonadas en la región tropical ha sido sujeto de múltiples estudios, así como de revisiones en las que se han identificado los patrones generales de cambio a través de la sucesión (Guariguata y Ostertag, 2001; Chazdon, 2003, 2008; Quesada *et al.*, 2009; Martínez-Ramos *et al.*, 2012). Puesto que el tiempo transcurrido desde el disturbio es un eje que integra el efecto de los procesos y mecanismos que ocurren durante la sucesión, la descripción de dichos patrones sucesionales se ha hecho con base en la relación entre la edad del bosque y los atributos florísticos, estructurales y funcionales del mismo. En general, existe una tendencia a la recuperación de la estructura (incluyendo biomasa), la diversidad y las funciones del ecosistema al incrementarse la edad del bosque, aunque existen diferencias importantes en la velocidad y trayectoria del proceso asociadas al atributo particular en cuestión (Figura 1.2).

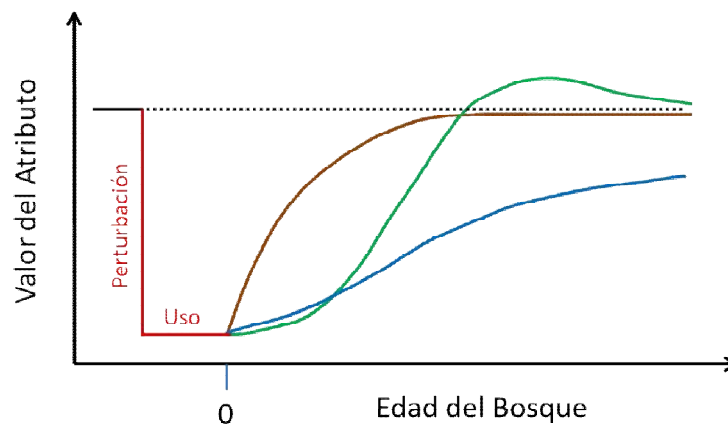


Figura 1.2. Recuperación idealizada de los atributos del bosque tropical a través de la sucesión secundaria en áreas agropecuarias. Cada una de las líneas de color representa una trayectoria de recuperación diferente, asociable en términos generales, a diferentes tipos de atributos del bosque: atributos estructurales (café), diversidad (verde), composición (azul). La línea punteada indica el valor del atributo en el bosque maduro previo a la perturbación.

Los atributos estructurales (área basal, altura de los árboles, densidad de individuos, cobertura del dosel e índice de área foliar, entre otros) muestran comúnmente una rápida recuperación hacia un valor asintótico, muy similar al de bosques maduros (Chazdon, 2008; Lebrija-Trejos *et al.*, 2010a), modificando a su vez las condiciones ambientales en los sitios (Chazdon, 2008; Lebrija-Trejos *et al.*, 2011; Pineda-García *et al.*, 2013). La diversidad de especies muestra también una clara tendencia de incremento, aunque la velocidad de recuperación es relativamente menor y presenta algunas veces valores máximos en edades

intermedias (Chazdon, 2008; Martin *et al.*, 2013). Por el contrario, la composición de especies puede mantenerse muy diferente aun después de décadas (Williamson *et al.*, 2012; Martin *et al.*, 2013) o converger rápidamente hacia la composición de especies propia de los bosques maduros (Norden *et al.*, 2009; Lebrija-Trejos *et al.*, 2010a). La diversidad funcional no presenta patrones claros de relación con la edad sucesional, aunque sí con el área basal (Lohbeck *et al.*, 2012). Funciones ecosistémicas como la productividad primaria tienden a incrementarse con la edad del bosque (Lawrence, 2005), mientras que la captura de C en la biomasa aérea presenta un patrón contrario (Yang *et al.*, 2011).

Si bien es posible generalizar la existencia de patrones de cambio a través de la sucesión secundaria en campos agropecuarios abandonados, existe también evidencia de que dichos patrones están relacionados con condiciones particulares de los sitios. Entre los factores que afectan las trayectorias sucesionales de recuperación se encuentran las condiciones ambientales (clima y suelo), la intensidad del disturbio asociado al uso agropecuario y la configuración del paisaje (Chazdon, 2008). El clima y el suelo actúan como factores que restringen la recuperación, al determinar los valores máximos alcanzables por los atributos (Recuadro 1.2), más que la velocidad relativa (resiliencia) del proceso (Becknell *et al.*, 2012; Martin *et al.*, 2013). Por el contrario, existe evidencia fuerte de que el incremento en la intensidad de uso reduce de manera importante la velocidad o incluso la trayectoria de la recuperación, particularmente para la diversidad y la composición de especies (Uhl *et al.*, 1982, 1988; Molina Colón y Lugo, 2006; Chazdon, 2008; Williamson *et al.*, 2012; Jakovac *et al.*, 2015), así como la productividad y la capacidad de acumular C (Hughes *et al.*, 1999; Zarin *et al.*, 2005; Lawrence *et al.*, 2007; Orihuela-Belmonte *et al.*, 2013). La cobertura de bosque presente en el paisaje, así como la cercanía del área en recuperación a los parches de bosque adyacentes también están asociadas positivamente con la trayectoria sucesional de la diversidad y composición de los sitios (Williamson *et al.*, 2012; Jakovac *et al.*, 2015).

Recuadro 1.2. *Un marco conceptual para el entendimiento de la sucesión vegetal.* La sucesión vegetal puede ser vista como un proceso integrador de otros que actúan a múltiples escalas espacio-temporales (Figura C.1.2.a; Walker & Wardle, 2014). Los procesos que ocurren a escalas espacio-temporales inferiores a las que se observa la sucesión pueden ser agrupados en tres grandes mecanismos sucesionales: la disponibilidad de áreas para la colonización, la disponibilidad de propágulos que colonicen y el comportamiento diferencial de las especies colonizadoras (Pickett *et al.*, 1987a, 1987b). Por otra parte, el proceso está restringido por factores de estado que operan a escalas superiores a las del fenómeno sucesional, entre los que se encuentran las condiciones climáticas y de suelo, así como los procesos de evolución biológica (Walker & Wardle, 2014). El régimen de disturbio actúa como factor modulador de los efectos de dichos procesos sobre la sucesión. En general, se espera que a medida que el disturbio reduce la calidad física y biológica de las áreas disponibles para la colonización o la disponibilidad de propágulos, la tasas de recuperación a través de la sucesión se reduzcan o las trayectorias sucesionales se vean alteradas (Figura C.1.2.b; Martínez-Ramos & García-Orth, 2007; Walker & Wardle, 2014).

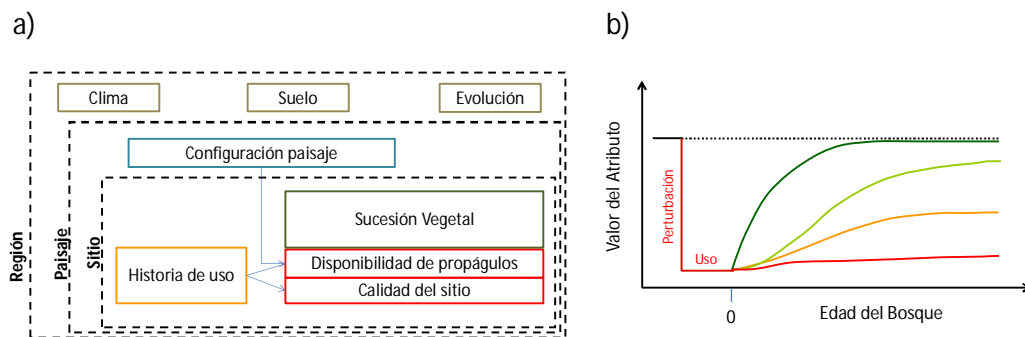


Figura C.1.2. Modelo conceptual de los factores que afectan la sucesión vegetal en las regiones tropicales luego del uso del suelo con fines agropecuarios. a) Modelo jerárquico de la sucesión, que integra el efecto de los principales factores que moldean la sucesión. Los factores a escala de sitio (historia de uso) y paisaje (configuración) determinan la trayectoria particular de la sucesión, mientras que los factores a escalas regionales restringen las posibilidades de la trayectoria sucesional. b) Trayectorias de recuperación idealizadas bajo diferentes condiciones de sitio. En general se espera que a mayor intensidad de uso y menor cobertura de bosque en la matriz adyacente, la velocidad a la que transcurre la recuperación sea menor (comparar líneas verdes) o más aún, que se modifique el máximo alcanzable a través de la sucesión (líneas roja y amarilla).

La cronosecuencia como aproximación metodológica

De importancia fundamental en el entendimiento de la sucesión en los bosques tropicales en áreas agropecuarias ha sido el uso de la aproximación metodológica conocida como cronosecuencia (Recuadro 1.1). La mayor parte de la evidencia actual sobre la sucesión secundaria en bosques tropicales proviene del uso de esta aproximación, a través de la cual la recuperación del bosque es inferida a partir de la asociación entre los atributos de los sitios y el tiempo transcurrido desde la perturbación (Pickett, 1989; Walker *et al.*, 2010). Esta aproximación presupone que los sitios se encuentran en condiciones biofísicas y tienen historias de uso similares. Sin embargo, las cronosecuencias han sido ampliamente criticadas, principalmente debido a su aparente imposibilidad de predecir de manera adecuada las tasas de cambio de los atributos a través de la sucesión y por ende las trayectorias sucesionales de los sitios particulares (Sheil, 2001; Feldpausch *et al.*, 2007; Johnson y Miyanishi, 2008; Maza-Villalobos *et al.*, 2011, pero ver también Foster y Tilman, 2000; Lebrija-Trejos *et al.*, 2010a). Dicha incoherencia puede estar asociada en parte a que el supuesto de homogeneidad de las condiciones en las que se encuentran los sitios es difícil de cumplir en ambientes espacialmente heterogéneos, donde las condiciones de manejo previas pueden ser igualmente heterogéneas (Balvanera *et al.*, 2002; Quesada *et al.*, 2009). Si bien la cronosecuencia constituye una fuente irremplazable de información para el estudio de procesos que ocurren en escalas de tiempo de décadas, como lo es la sucesión secundaria en los trópicos (Quesada *et al.*, 2009; Walker *et al.*, 2010), estos resultados resaltan la necesidad de complementarla mediante el uso de métodos y aproximaciones alternativas, tales como el uso de anillos de crecimiento para determinar la edad de los sitios (Brienen *et al.*, 2009; Sierra *et al.*, 2012), la caracterización de la historia previa de uso de los mismos (Jakovac *et al.*, 2015), o su seguimiento a través del tiempo (Chazdon *et al.*, 2007). La integración de dichas alternativas permitirá lograr un mejor entendimiento de la dinámica sucesional y de los factores que la moldean.

Bosques tropicales secos, sucesión y almacenes de carbono

El BTS constituye uno de los principales ecosistemas tropicales. Este ecosistema comprende entre 36 y 48 % del área de bosque tropical y está representado en cuatro continentes (Malhi y Grace, 2000; Mayaux *et al.*, 2005; Achard *et al.*, 2014). Como en el caso de los bosques tropicales en general, el BTS ha sido extensivamente transformado, principalmente para actividades agropecuarias (Burgos y Maass, 2004; Sánchez-Azofeifa y Portillo-Quintero, 2011), cubriendo actualmente cerca de un millón de km² (Miles *et al.*, 2006), lo que representa tan sólo entre 34 y 51 % de su distribución original (Hoekstra *et al.*, 2004;

Sánchez-Azofeifa y Portillo-Quintero, 2011). Además, dicha transformación ha generado paisajes con un alto grado de fragmentación de la matriz original de bosque (Miles *et al.*, 2006), en los que áreas agrícolas y pecuarias activas y abandonadas, relictos de bosque no perturbado, bosques en uso y bosques secundarios en diferente estado de sucesión se mezclan formando un complejo mosaico de coberturas vegetales (Chazdon, 2014).

La particularidad de la sucesión en el BTS

El BTS ha sido comúnmente visto como un sistema con una alta resiliencia, asociada a la su relativa simplicidad estructural, a su menor diversidad taxonómica y la presencia de un elevado número de especies con capacidad para rebrotar cuando se le compara con el bosque tropical húmedo (Murphy y Lugo, 1986). Sin embargo, los estudios en torno a la sucesión secundaria en campos agropecuarios en regiones estacionalmente secas indican que la recuperación del BTS sigue patrones similares a los descritos para el bosque tropical húmedo (Lebrija-Trejos *et al.*, 2008; Martin *et al.*, 2013). A pesar de ello, desde una perspectiva funcional la recuperación parece ser diferente. El remplazamiento de especies de árboles en el BTS a través de la sucesión parece reflejar cambios en sus estrategias funcionales, desde especies que evitan la sequía propia de los ambientes sucesionales tempranos, a especies que toleran dicha deficiencia en ambientes sucesionales tardíos (Lohbeck *et al.*, 2015a). Atributos funcionales como el rebrote parecen tener una mayor incidencia e incidir de manera importante sobre la recuperación (Vieira y Scariot, 2006; Lévesque *et al.*, 2011). Adicionalmente, el número de grupos funcionales de especies en relación a su afinidad sucesional parece estar restringido a sólo dos grupos: especies pioneras, comúnmente leguminosas de los géneros *Acacia* y *Mimosa*, y especies características del bosque maduro (Álvarez-Yépez *et al.*, 2008; Lebrija-Trejos *et al.*, 2010a).

Almacenes de carbono y tasas de captura a través de la sucesión en el BTS

Asociados a la recuperación de la estructura, los almacenes de C en la biomasa aérea muestran también una tendencia a la recuperación a través de la sucesión secundaria en el BTS¹ (Marin-Spiotta *et al.*, 2008; Vargas *et al.*, 2008; Hernández-Stefanoni *et al.*, 2010; Becknell *et al.*, 2012; Martin *et al.*, 2013). Se estima que entre 60 y 80 % del C en este compartimento se ha recuperado al cabo de 30 años de abandono (Romero-Duque, 2008; Vargas *et al.*, 2008), mientras que la recuperación total del almacén ocurre posiblemente al

¹ En esta revisión se incluyen también los trabajos que estiman biomasa, debido a la estrecha relación que guardan estas dos variables y a posibilidad de convertir dichos valores en almacenes de carbono empleando factores de conversión conocidos (Jaramillo *et al.*, 2003a)

cabo de 100 años (Read y Lawrence, 2003). La tasa de acumulación de C parece ser máxima en los primeros 5 a 10 años de abandono de la actividad agropecuaria, reduciéndose al avanzar la sucesión (Vargas *et al.*, 2008).

Los estudios sobre los almacenes de C en otros compartimentos del ecosistema son mucho más escasos, lo que impide hacer generalizaciones respecto a su recuperación a través de la sucesión secundaria (Marin-Spiotta *et al.*, 2008; Kauffman *et al.*, 2009; Jaramillo *et al.*, 2011). El C en la biomasa aérea muerta parece presentar valores mínimos para estados intermedios de la sucesión y no en estados iniciales como ocurre en la biomasa aérea viva, debido a la presencia de una importante cantidad de material muerto justo después del desmonte (Read y Lawrence, 2003; Kissing y Powers, 2010). Por otra parte, no existen estudios que cuantifiquen el C en la biomasa de raíces a través de la sucesión (Marin-Spiotta *et al.*, 2008). Estudios puntuales indican que éste puede alcanzar hasta un 75 % de su valor original después de 30 años de recuperación (Romero-Duque, 2008), mientras que las raíces finas pueden (Vargas *et al.*, 2008) o no (Powers y Pérez-Aviles, 2012) incrementar su biomasa a través del tiempo. La evidencia respecto a la recuperación del C en el suelo también es equívoca. En términos generales, el C en la materia orgánica del suelo se incrementa con el cambio de uso de suelo de áreas agropecuarias a bosque secundario (Don *et al.*, 2011). Sin embargo, no existe una relación consistente entre la edad del bosque y el C en suelo entre sitios (Saynes *et al.*, 2005; Gamboa *et al.*, 2010; pero ver Vargas *et al.*, 2008), posiblemente como consecuencia de dificultades metodológicas en la detección de los cambios, o a una mayor resistencia al cambio de este almacén (Marin-Spiotta *et al.*, 2008). En conjunto, estos resultados indican la necesidad de cuantificar los almacenes de C ecosistémico a lo largo de todo el proceso sucesional en el BTS, con el fin de poder establecer cuáles de los compartimentos se recuperan a través de la sucesión y en qué momento del proceso ocurre la recuperación. Más aún, la estimación de las tasas de captura de C no ha sido hasta ahora objeto de estudio de ninguno de los trabajos precedentes (pero ver Vargas *et al.*, 2008), a pesar de su relevancia en el contexto de la incertidumbre asociada a las estimaciones de flujos de C en las regiones tropicales y la mitigación del cambio climático, como se mencionó anteriormente.

Factores que afectan la recuperación de los almacenes de C durante la sucesión

Los almacenes de C en el BTS secundario cambian no sólo a través del tiempo, sino del paisaje, como resultado de las diferencias en las condiciones biofísicas en las que se encuentran los sitios, y de su historia de uso, las cuales además no son independientes entre sí (Burgos y Maass, 2004). En el contexto del ciclo del C, es importante entender el

efecto que tienen estos factores sobre las tasas de captura de C y la capacidad máxima de almacenamiento de C en los bosques tropicales (Kauffman *et al.*, 2009). El clima y el suelo actúan como factores que restringen el tamaño máximo de los almacenes de C en la biomasa aérea (Recuadro 1.2.), a través de su efecto sobre la estructura de la vegetación, siendo mayores al aumentar la precipitación y al reducirse el déficit hídrico (Stegen *et al.*, 2011; Durán *et al.*, 2015; pero ver Baraloto *et al.*, 2011). Tanto el aumento en la disponibilidad de agua como de nutrientes están asociados a mayores valores absolutos de acumulación de C durante la sucesión (Marin-Spiotta *et al.*, 2008; Kauffman *et al.*, 2009; Becknell *et al.*, 2012), aunque no con la recuperación relativa a los niveles de referencia en los bosques maduros (Martin *et al.*, 2013). Los almacenes subterráneos y su cambio en el tiempo también parecen estar relacionados con el nivel de fertilidad del suelo (Gamboa *et al.*, 2010; Powers y Pérez-Aviles, 2012).

La diversidad biológica puede jugar un papel importante en la definición de las trayectorias de recuperación de los almacenes de C durante la sucesión. Diversos aspectos de la diversidad de árboles, tales como el número de especies o los valores comunitarios de atributos funcionales particulares, se asocian con la magnitud de los almacenes de C y con la acumulación de biomasa en los bosques tropicales secundarios (Barrufol *et al.*, 2013; Conti & Díaz, 2013; Lasky *et al.*, 2014; Lohbeck *et al.*, 2015b). Sin embargo, la diversidad comúnmente cambia a través de la sucesión (Lebrija-Trejos *et al.*, 2010a; Lohbeck *et al.*, 2013; Martin *et al.*, 2013), por lo que la simple correlación entre variables no proporciona evidencia suficiente de un efecto funcional (Lohbeck *et al.*, 2015b). Por ende, se requieren estudios que evalúen de manera conjunta los efectos de la edad del bosque y la diversidad de plantas en la recuperación de los almacenes de C. Este tipo de estudios no existen aún en el caso del BTS.

Las características del disturbio asociado al cambio de uso de suelo para actividades agropecuarias también constituyen un factor que moldea la trayectoria sucesional de recuperación de los almacenes de C. Dicho efecto puede ser entendido a través del análisis de dos ejes de variación del régimen de disturbio: la intensidad, que integra la duración y frecuencia del uso, y el tipo de uso. La intensidad del uso agropecuario es uno de los factores que más influyen en la recuperación de los almacenes de C durante la sucesión de bosques tropicales (Marin-Spiotta *et al.*, 2008; Kauffman *et al.*, 2009; pero ver Martin *et al.*, 2013). Las tasas de recuperación de C en la biomasa aérea se reducen al incrementarse la duración o la frecuencia del uso agropecuario (Hughes *et al.*, 1999; Zarin *et al.*, 2005; Lawrence *et al.*, 2007, 2010; Orihuela-Belmonte *et al.*, 2013). Por su parte, el tipo de uso previo al abandono de las actividades agropecuarias parece definir tanto la pérdida inicial de C durante la conversión del bosque, como la acumulación de C durante la sucesión. La

deforestación para uso agrícola causa una mayor pérdida del C orgánico del suelo que el establecimiento de potreros (Don *et al.*, 2011; Powers *et al.*, 2011), mientras que durante la sucesión la acumulación de C es mayor en sitios sólo deforestados, menor para sitios agrícolas y sin relación aparente con la edad del bosque en potreros (Marin-Spiotta *et al.*, 2008; Don *et al.*, 2011; Powers *et al.*, 2011) la biomasa aérea sigue un patrón similar (Marin-Spiotta *et al.*, 2008). Más aún, el tipo e intensidad de uso pueden estar espacialmente asociados a la condiciones biofísicas (Burgos y Maass, 2004; Mwampamba y Schwartz, 2011). Por otra parte, el uso del bosque durante su recrecimiento, que incluye el aprovechamiento de recursos forestales maderables y no maderables, así como el pastoreo, puede reducir también la acumulación de C (Mwampamba, 2009; Chaturvedi *et al.*, 2012).

En síntesis, el entendimiento de la variabilidad en los almacenes de C en paisajes transformados implica no sólo el reconocimiento del tiempo sucesional como una variable fundamental, sino también de la variación espacial en las condiciones ambientales y en el tipo e intensidad del uso de los sitios (Urquiza-Haas *et al.*, 2007; Hernández-Stefanoni *et al.*, 2010; Berenguer *et al.*, 2014). Este tipo de evaluaciones a escala de paisaje son aún limitadas para el caso del BTS.

El bosque tropical como herramienta de mitigación del cambio climático

En el contexto del cambio climático global, tanto el elevado potencial de captura de C en la biomasa de los bosques tropicales, como la condición de fuente de gases de efecto invernadero (GEI) por transformación de bosques, hacen de las regiones tropicales herramientas potenciales de mitigación del cambio climático. El potencial de captura de C constituye la base de proyectos de forestación y reforestación implementados en el marco del Mecanismo de Desarrollo Limpio asociado al Protocolo de Kioto, en vigor desde 2005. Por su parte, la reducción de emisiones de GEI derivadas de la transformación de los bosques constituye el objetivo de REDD+ (Reducing Emissions from Deforestation and Forest Degradation, por su sigla en inglés), un instrumento económico de pago por servicios ambientales que se encuentra en negociación desde el año 2007 (UNFCCC, 2008, 2010).

La implementación del programa REDD+ supone la existencia de beneficios adicionales a las reducciones de emisiones de GEI, entre los que se encuentran la reducción de la pobreza, una mejor gobernanza de los recursos forestales y la conservación de la biodiversidad (Angelsen, 2008; Parrotta *et al.*, 2012). Puesto que la deforestación y la degradación se concentran en la región tropical y constituyen también la principal causa de pérdida de la diversidad biológica en la región (Myers *et al.*, 2000; Wright *et al.*, 2006; Laurance, 2007), la reducción de las emisiones de GEI asociadas puede implicar

adicionalmente la conservación de dicha biodiversidad (Miles y Kapos, 2008; Grainger *et al.*, 2009). La consecución de ambos objetivos requiere de la identificación de áreas adecuadas para la reducción de emisiones de GEI y para la conservación de la biodiversidad, la identificación de las actividades de manejo idóneas para dichas áreas, así como el planteamiento de estrategias que permitan evitar que la deforestación y degradación se fuguen a otras regiones (Miles y Kapos, 2008; Phelps *et al.*, 2012a, 2012b).

En este sentido, un elemento fundamental para la implementación de REDD+ es el reconocimiento de que los paisajes tropicales actuales constituyen un mosaico de diferentes coberturas vegetales asociadas a múltiples historias de manejo y a diferentes tiempos de desarrollo sucesional (Figura 1.1) (Chazdon, 2014). La deforestación y la degradación son procesos que afectan no sólo a los bosques maduros, sino también a los bosques transformados o secundarios (Figura 1.1). Estos bosques también constituyen reservorios de diversidad y contribuyen a su mantenimiento a escala de paisaje (Castillo-Campos *et al.*, 2008; Gardner *et al.*, 2009; Chazdon *et al.*, 2011a). Por ende, la evaluación de las sinergias entre conservación y reducción de emisiones requiere entonces del análisis del paisaje en su conjunto, a partir del reconocimiento de la variación espacial de los almacenes de C y de la diversidad biológica, en particular en relación a las diferentes condiciones ambientales y de uso que dieron origen a dicha variación.

Presentación de la tesis

El objetivo principal de esta tesis fue la evaluación de los factores que afectan la recuperación de la estructura, de la diversidad y de los almacenes de carbono a través de la sucesión secundaria en campos agropecuarios abandonados en un paisaje de BTS (Figura 1.3.), utilizando para ello una combinación de aproximaciones estática (cronosecuencia) y dinámica (mediciones repetidas a través del tiempo). Los objetivos particulares fueron:

1. Establecer cómo cambia la estructura, la diversidad y la composición de la comunidad de árboles a través de la sucesión secundaria del BTS, poniendo a prueba la capacidad de la aproximación de cronosecuencia para explicar y predecir su dinámica a través del tiempo.
2. Evaluar la recuperación de los almacenes de carbono del BTS a través de la sucesión, poniendo a prueba la capacidad explicativa de la edad del bosque y la diversidad de árboles sobre la magnitud de los almacenes de carbono y su cambio a través del tiempo.

3. Cuantificar la asociación entre los almacenes de carbono y la diversidad de árboles en bosques secundarios a través del paisaje, poniendo a prueba el efecto del régimen de disturbio de los sitios y de los atributos del espacio (topografía y configuración del paisaje) sobre dicha asociación, y evaluando sus implicaciones para la implementación del mecanismo REDD+.

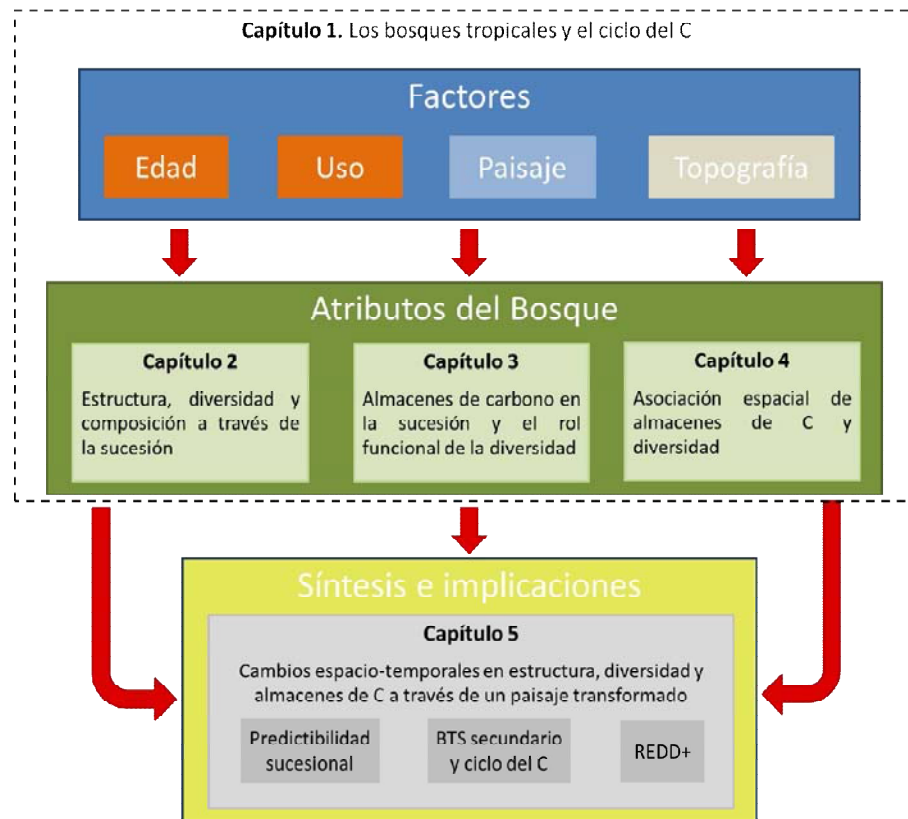


Figura 1.3. Estructura del presente trabajo de tesis.

La tesis consta de cinco capítulos. En este primer capítulo introductorio se presentan los elementos conceptuales y antecedentes necesarios para el desarrollo de la tesis. En cada uno de los capítulos 2 al 4 se pone a prueba al menos uno de los factores que potencialmente explican la variación en los atributos del bosque (Figura 1.3.). En el Capítulo 2 se aborda el primer objetivo, esto es, la descripción de los patrones de recuperación sucesional de diferentes tipos de atributos de la comunidad de árboles. El segundo objetivo, referente a la cuantificación de los almacenes de C ecosistémico en bosques secundarios y su recuperación a través de la sucesión, se aborda en el Capítulo 3. El tercer objetivo sobre la asociación entre almacenes de C aéreos y la diversidad de especies a través del paisaje, se examina en el Capítulo 4. En el capítulo final se hace una síntesis de los factores que

determinan la variación espacial y temporal de la estructura, diversidad y almacenes de C y sus implicaciones teóricas y prácticas (Figura 1.3.).

Área y sistema de estudio

Esta investigación se desarrolló en la región de Chamela-Cuixmala, ubicada en la costa del Pacífico mexicano, en el estado de Jalisco ($19^{\circ}23'$ - $19^{\circ}30'N$, $104^{\circ}56'$ - $105^{\circ}04'O$, Ceballos y García, 2010). La región se caracteriza por su clima estacionalmente seco, con una temperatura media anual de $24.6^{\circ}C$ y una precipitación media anual (entre 1983 y 2013) de 756 mm, concentrada entre junio y octubre (datos del proyecto "Cuencas", IIES, UNAM). El tipo de ecosistema predominante en la región es el BTS, aunque asociado a diferentes condiciones topográficas es posible definir variaciones locales en el tipo de cobertura vegetal. En las colinas y montañas el tipo de cobertura vegetal original es la selva baja caducifolia (*sensu* Miranda y Hernández-X, 1963; Durán *et al.*, 2002), mientras que las planicies de inundación de los ríos mayores, así como la ribera de los cauces de tamaño medio se encontraban originalmente cubiertas por selva mediana subcaducifolia (*sensu* Miranda y Hernández-X, 1963; Durán *et al.*, 2002).

El área de estudio corresponde a una franja paralela a la línea de costa, de aproximadamente 50 km de largo \times 20 km de ancho, que corre en dirección sureste-noroeste (Figura 1.3.). El límite norte corresponde al río San Nicolás, mientras que al sur se encuentra delimitada por el río Purificación. El estudio se restringió a áreas ubicadas por debajo de 300 m snm. En el centro de la región se ubica la Reserva de la Biósfera Chamela-Cuixmala, de 13.142 ha de extensión (Ceballos y García, 2010), entre el arroyo Chamela y el río Cuitzmala. La reserva se encuentra rodeada principalmente por tierras ejidales, pertenecientes a ocho ejidos del municipio de La Huerta (Sánchez-Azofeifa *et al.*, 2009).

La región tiene una historia de asentamiento en tiempos modernos muy reciente. El principal flujo de migrantes a la región ocurrió entre finales de la década de 1960 y principios de la de 1970, como resultado de la constitución de ejidos en la región (Castillo *et al.*, 2005). El establecimiento de los ejidos conllevó a la transformación progresiva del BTS para el establecimiento de áreas de cultivo en las planicies de inundación y riberas de los ríos y arroyos, y de pastizales para la crianza de ganado en las zonas colinas (Burgos y Maass, 2004). Sin embargo, debido tanto a reducciones en la productividad de las parcelas como a cambios socio-económicos a nivel nacional, algunas áreas han sido abandonadas (ver Recuadro 1.1), lo que conlleva al desarrollo de bosques secundarios a través de un proceso de regeneración natural (Burgos y Maass, 2004). En la actualidad, como resultado de la acción de dichos procesos de transformación durante más de cuatro décadas, entre 70 y 80

% de la región se encuentra cubierta por bosques tropicales maduros y bosques secundarios en distintas etapas de desarrollo, entre 16 y 28 % por pastizales, y tan sólo 2 % corresponde a por áreas de cultivo activas, comúnmente ubicadas en las zonas planas (Sanchez-Azofeifa *et al.*, 2009; Cohen, 2014; F. Mora, datos no publicados). El BTS está bajo el manejo de las comunidades locales, excepto por los predios correspondientes a la Reserva de la Biosfera, los cuales están dedicados casi en su totalidad a la conservación biológica y a la investigación científica. El manejo local incluye la extracción de productos forestales maderables y no maderables, así como el ramoneo de ganado vacuno (Burgos y Maass, 2004; Rendón-Carmona *et al.*, 2009; Cohen, 2014).



Figura 1.4. Área de estudio. El estudio se desarrolló en la región de Chamela-Cuixmala, principalmente entre los ríos San Nicolás y Purificación, en el municipio de la Huerta, Jalisco, México. Los puntos rojos corresponden a la ubicación particular de los sitios incluidos en el estudio. Imágenes tomadas de Google Earth®.

El sistema de estudio

El estudio se realizó empleando dos conjuntos de sitios diferentes. Todos los sitios se ubicaron en los alrededores de la Reserva de la Biósfera de Chamela-Cuixmala, excepto por

algunos sitios ubicados al interior de la reserva. Los estudios correspondientes a los Capítulos 2 y 3 se desarrollaron en un conjunto de 12 sitios establecidos en el marco del proyecto de investigación Manejo de Bosques Tropicales "MABOTRO", los cuales constituyen la base de un sistema de estudio permanente sobre la sucesión secundaria en campos agropecuarios abandonados (Martínez-Ramos *et al.*, 2012). En cada sitio se estableció, desde el año 2004, una parcela de 30 x 60m dentro de la cual se marcaron y midieron todos los árboles, empleando para ello un muestreo estratificado con base en categorías de diámetro a la altura del pecho (DAP); desde 2004 se realizan censos de la vegetación cada tres años.

El estudio correspondiente al Capítulo 4 se realizó incluyendo un segundo conjunto de 38 sitios que fueron seleccionados para ampliar el intervalo de variación de aquellos incluidos en los sitios MABOTRO, en lo concerniente tanto a las condiciones biofísicas (se incluyeron sitios en zonas planas correspondientes a valles de ríos y áreas de inundación), como a la historia de uso (sitios hasta de 42 años de abandono, que incluyen sitios desmontados con maquinaria pesada y que presentan en la actualidad diferentes grados de uso, tanto de extracción de productos maderables como de ingreso del ganado). La vegetación fue caracterizada entre 2013 y 2014, siguiendo un protocolo modificado de Baraloto *et al.* (2013). En ellos se establecieron cinco parcelas (no permanentes) rectangulares de 5 × 50 m, paralelas entre sí y separadas por una distancia de 15 m. Se realizó un muestreo estratificado por categorías de DAP.

Capítulo 2. *Testing chronosequences through dynamic approaches:
Time and site effects on tropical dry forest succession*

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Abstract

Chronosequences, commonly used to assess succession, have been questioned because of their failure to project successional trajectories. Here, we develop a simple analytical approach combining both chronosequence and dynamic data to test the power of age of abandonment and site factors to explain and predict succession. The approach proceeds by first fitting statistical models relating age to attribute values (the chronosequence model) and their observed changes (the dynamic model) to test explanatory power. Predictive power is then tested by bootstrapping the chronosequence model to derive confidence intervals for expected changes and comparing them with the dynamic model. Finally, residuals from both models are tested against site factors. The procedure was applied to six attributes (basal area, plant density, mean plant height, species richness, evenness, and composition) of the woody community (plants > 1 cm diameter at breast high within 0.1 ha plots) in nine abandoned cattle pastures (0-12 yr) and three old-growth tropical dry forests monitored over 6 yr. Age explained 60-97 % of the variance in community attributes and only 32-57 % in observed changes. It significantly overestimated basal area and mean height, while species richness and composition were highly predicted. Besides age, management history also explained successional dynamics. Our results suggest age is not necessarily a reliable predictor of short-term successional dynamics, and explanatory power is not indicative of predictive power. Because of this low reliability, caution is needed when applying chronosequences to evaluate ecosystem services' recovery. The analytical approach developed here contributes to a better exploration of those possible limitations.

Key words: Chamela; land use history; Mexico; nonlinear models; rates of change; soil conditions; successional trajectories; surrounding matrix.

Introduction

Secondary forests will likely dominate future tropical landscapes. Old-growth tropical forests have been transformed mainly for the expansion of agriculture (Geist y Lambin, 2002; Sánchez-Azofeifa y Portillo-Quintero, 2011), but agricultural fields are often subsequently abandoned because of productivity loss or change in socioeconomic context (Wright, 2005). Secondary forests developing in these abandoned fields are becoming increasingly representative of tropical landscapes, reclaiming up to one-third of the original deforested area (Wright, 2005; Foley *et al.*, 2007). Understanding how these forests change in the course of succession is critical for ensuring biodiversity conservation and maintaining the supply of ecosystem services in tropical regions (Barlow *et al.*, 2007; Chazdon *et al.*, 2009a, 2009b).

Research on secondary succession in abandoned agricultural fields has mostly relied on the use of the chronosequence approach, where successional change is inferred by relating the time since field abandonment to plant community attributes such as basal area, biomass or species richness (Pickett, 1989; Walker *et al.*, 2010). The chronosequence approach, however, has been challenged (Johnson y Miyanishi, 2008). First, there is large variation in the explanatory power of age of abandonment, associated with differences in previous use or environmental conditions among sites (Marin-Spiotta *et al.*, 2008; Mwampamba y Schwartz, 2011; Dupuy *et al.*, 2012), or with the community attribute being analyzed (Chazdon, 2008; Lebrija-Trejos *et al.*, 2008; Muñoz-Castro *et al.*, 2011). Second, there is an apparent inability to project successional trajectories, since changes over time in ecosystem attributes do not necessarily match successional trajectories or rates of change inferred from chronosequences (Foster y Tilman, 2000; van Breugel *et al.*, 2006; Chazdon *et al.*, 2007; Feldpausch *et al.*, 2007; Maza-Villalobos *et al.*, 2011). These challenges raise questions about the particular situations and variables for which chronosequences would adequately describe successional change (Walker *et al.*, 2010) and, therefore, about its applicability to project the recovery of ecosystem attributes such as biomass and carbon stocks (Feldpausch *et al.*, 2007; Johnson y Miyanishi, 2008).

An improved understanding of succession could be achieved if chronosequences were complemented with a dynamic approach by monitoring sites through time, allowing for a test of the match between successional trajectories projected from chronosequences and those derived from repeated measurements (Pickett, 1989; Foster y Tilman, 2000; Chazdon *et al.*, 2007); however, there are relatively few dynamic studies of tropical succession (Chazdon *et al.*, 2007; Lebrija-Trejos *et al.*, 2010a; Williamson *et al.*, 2012). In addition, there is a lack of adequate, statistically-based tests for chronosequence-based inferences (Feldpausch *et al.*, 2007; Johnson y Miyanishi, 2008). Tests have mostly relied on

the visual comparison of the trajectories from chronosequence and dynamic observations or on correlations between age of abandonment and observed community changes (Foster y Tilman, 2000; Chazdon *et al.*, 2007; Maza-Villalobos *et al.*, 2011; Williamson *et al.*, 2012); these approaches do not test for specific trajectories or rates of change expected from chronosequence models.

The effect of site factors should also be taken into account to improve our understanding of succession. There is extensive evidence suggesting that factors like field management history, soil properties, and adjacent forest cover can influence succession (Holl, 1999; Guariguata y Ostertag, 2001; Chazdon, 2003, 2008). Their effects may depend upon the attribute analyzed. Species diversity and composition are expected to be dependent primarily on both the presence of remnant vegetation, and on the properties of the forest matrix around sites (Purata, 1986; Holl, 1999; Norden *et al.*, 2009). On the other hand, structural attributes have shown to be highly influenced by previous land use, particularly the type of land clearance or the frequency of fires (Uhl *et al.*, 1988; Moran *et al.*, 2000), although they can also influence species composition (Mesquita *et al.*, 2001). Most of the chronosequence studies, however, rely on the assumption that sites are under similar conditions, and only a few have addressed those site effects, particularly for tropical dry forests (Uhl *et al.*, 1982, 1988; Moran *et al.*, 2000; Powers *et al.*, 2009; Mwampamba y Schwartz, 2011; Dupuy *et al.*, 2012). Since chronosequence's failure to project successional dynamics could be explained by subtle differences in site conditions, testing this assumption is relevant in explaining successional patterns and the usefulness of the chronosequence approach.

To advance in the understanding of the power of age of abandonment and site conditions to explain and predict changes in forest attributes along succession, in this paper we developed a model-based analytical approach combining chronosequence and dynamic data to test chronosequence explanatory power and its predictions of successional dynamics. We then applied this procedure to study secondary succession of tropical dry forest (TDF) woody communities in abandoned cattle ranching pastures of western Mexico. Six different community attributes were analyzed: basal area, plant density, height, species richness, species evenness, and species composition. We further assessed the role of site factors like field management history, soil condition, and adjacent forest cover in explaining successional patterns of these attributes. Specifically, we tested the following: (1) whether age of abandonment is a major explanatory variable of among-site variability in community attributes and their observed net changes, (2) to what extent chronosequence models predict net changes in community attributes observed over 6 yr, and (3) to what extent site

factors other than age of abandonment explain variability in community attributes and their observed changes over time.

Methods

Analytical approach

The main hypothesis behind the chronosequence approach is that time since field abandonment constitutes a major explanatory variable for differences in community attributes across sites. Testing this hypothesis commonly proceeds through fitting a statistical model relating the observed chronosequence data to age of abandonment (*i.e.* a chronosequence model). If chronosequence assumptions were met (sites are under the same biophysical conditions and subjected to similar management regime), we would expect site dynamics to parallel the trajectory or present a trend similar to that predicted by the chronosequence model. Consequently, a test of the predictive power of a chronosequence could proceed by calculating observed community changes from repeated measurements over a given time period and comparing them with expected changes derived from the chronosequence model. Here we develop and apply an analytical approach following this rationale.

The analytical approach can be summarized in seven steps. In step 1, a chronosequence model is fitted to explore whether age of abandonment explains variability in attribute values among sites. In step 2, a confidence interval for the chronosequence model is calculated from a family of fitted models generated by bootstrapping samples. Step 3, expected net changes in attribute (NC_{exp}) are calculated from the chronosequence model as $NC_{exp} = A_{t+\Delta t} - A_t$, where A_t is the attribute value calculated from the model at a given age (time = t), and $A_{t+\Delta t}$ is the value of such a trait after Δt yr. Step 4, confidence intervals for the NC_{exp} are obtained by applying step 3 to the family of models from bootstrapped samples obtained in Step 2. Step 5, observed net changes in attribute (NC_{obs}) for each site are calculated as the difference between two repeated measurements separated by the Δt period. A “net change model” relating NC_{obs} to age at first measurement is then fitted to explore to what extent age explains variability in observed net changes among sites. Step 6, test of the predictive power of the chronosequence on the observed successional dynamics is done by comparing the mean and confidence intervals for NC_{exp} (steps 3 and 4) with the net change model (step 5). Step 7, linear models are used to relate residuals from the chronosequence and net change models to site variables in

order to assess the importance of site factors on succession beyond age effects. Further details on the analytical approach and an R code for its implementation are provided in Appendix S2.1.

Test of the chronosequence using tropical dry forest data

We applied the analytical approach to a case study of TDF secondary succession conducted in the Chamela-Cuixmala Biosphere Reserve (CCBR) and adjacent areas, on the Pacific coast of the state of Jalisco, Mexico (19°23′- 19°30′N, 104°56′- 105°04′W). Mean annual temperature is 24.6°C, and mean annual precipitation is 788mm, with a severe drought season from November to May (García-Oliva *et al.*, 2002). Because of rainfall seasonality, most of the landscape is covered by TDF from 5 to 10 m high (Sánchez-Azofeifa *et al.*, 2009). Areas adjacent to the CCBR have been transformed mainly into pastures for cattle raising during the past 40 yr (Maass *et al.*, 2005). Those areas are often left without maintenance, resulting in the development of secondary forests (Burgos y Maass, 2004).

A chronosequence was established with nine secondary forests from abandoned pastures and three old-growth forests sites (without evidence of recent human disturbance). Sites were located at northwest and southeast extremes of the CCBR in order to include possible regional variations in climate or soils associated with geologic origin or topography (García-Oliva *et al.*, 2002; Schaaf, 2002). All of the sites were located on slopes (15° to 30°) to represent the dominant topographic condition (Balvanera *et al.*, 2002; Cotler *et al.*, 2002) and faced south (southeast to southwest) to represent the most extreme conditions in terms of high evaporative demand (Balvanera *et al.*, 2002). All secondary forests were located in sites where land was used mainly for cattle ranching (from 4 to 28 yr after slash and burn of the former old-growth forest) with repeated burning, planting of exotic grasses and free grazing. Age of abandonment varied between 0 and 12 yr by November 2004 (assessed through interviews with owners), when permanent plots were established and sites fenced with barbed wire to exclude cattle.

At each site a 20 × 50 m plot was established. All woody plants including trees, shrubs and lianas, and arborescent cacti (henceforth all will be referred to as woody community) were tagged, identified and measured for diameter at breast height (DBH) in 2004 (we measured the diameter at the base for lianas, which will be hereafter referred to for all as DBH). Plant height was measured since 2007 (excepting lianas). A size-stratified sampling was used: stems with DBH ≥ 1cm were sampled in half of the plot (10×50 m) and those ≥ 2.5cm DBH in the other half. Two additional censuses were carried out in 2007 and 2010 following the same sampling protocol.

For each plot and census year, we assessed structural attributes, as well as species diversity and species composition. Structural attributes included basal area, plant density and plant mean height (the latter only for plants with at least one stem > 2.5cm DBH). Diversity attributes were rarefied species richness (for 50 individuals per plot) and evenness (using Hurlbert's Probability of Inter-specific Encounter), both calculated using EcoSim (Gotelli y Entsminger, 2011). Species composition was reduced to a continuous scale by applying a non-metric multidimensional scaling ordination (NMDS) to a Chao-Sorensen matrix of dissimilarities for the data from the three censuses and 12 sites; site scores for the first ordination axis were then employed to represent species composition for each site/year combination. Stress value obtained was 0.021. NMDS was performed using the "metaMDS" function in the vegan package for R (Oksanen *et al.*, 2011).

Chronosequence models in step 1 were fitted using data from 2004. For each attribute, four different nonlinear models were tested: Michaelis-Menten, asymptotic, Gompertz and logistic (Table S2.1). In all models, old-growth sites were included by setting their age as 100 yr, since model parameter estimates did not change by more than 0.1 % when old-growth forest age varied between 50 and 500; other studies have used a similar criterion (Peña-Claros, 2003; Becknell *et al.*, 2012). Model fitting was performed using "nls" function in R (R Development Core Team, 2011). The best fitted model for each community attribute was selected based on the AICc. For the net change models, the form of the model corresponded to the first derivative of the best-fitted chronosequence model (Table S2.1). Confidence intervals for model parameters were calculated based on 1000 bootstrapped samples for each model. Observed and expected net change (NC) in steps 3 to 5 were calculated for $\Delta t = 6$ for all attributes except mean plant height, in which case $\Delta t = 3$ yr.

Residuals from both the chronosequence models and the net change models were related to field management history, soil condition, and adjacent forest cover of the sites (step 6). Management previous to plot establishment, characterized through semi-structured interviews with landowners (Trilleras, 2008), was summarized into variables describing the frequency, magnitude, intensity and duration of agricultural, pastoral and extractive activities (Appendix S2.3). Physical and chemical soil properties as well as soil degradation status were assessed from one soil profile in each site (Appendix S2.3; Trilleras 2008). Adjacent forest cover (by differentiating forested and non-forested areas) was quantified using true color imagery from 2003, downloaded from Google Earth® and interpreted using Arcmap® for buffers of 100-300 m (Appendix S2.3); these distances cover the spatial range at which most seed wind dispersal occurs (Contreras-Sánchez *et al.*, 2011).

Site variables were subject to an ordination procedure in order to reduce their dimensionality and to ensure orthogonality. Ordination was performed using the "dudi.mix"

function in the *ade4* package for R (Dray y Dufour, 2007), which allows for the inclusion of continuous, ordinal and categorical data in the same analysis. Residuals from models were then related to ordination axes using linear models. The first three ordination axes, which explain 57.5 % of variation in site variables, were tested (Table S2.2). We used the “*Imp*” function in the *lmPerm* package for R (Wheeler, 2010), which employs permutation tests to obtain *P*-values for the models without assuming normality. We included only the nine secondary forests in this analysis since management was meaningless for old-growth forests. Finally, pairwise associations were tested among residuals from chronosequence models or net change models and those site variables that significantly correlated to the ordination axes. Associations were tested using Spearman correlations when site variables were quantitative or ordinal and correlation ratios when categorical. Because of the high number of site variables included in the analysis of pairwise associations (33 variables correlated to axis 1 through 3, shown in Table S2.2), an inflated probability of rejecting the general null hypothesis of no site effects could arise. Bonferroni corrections were then applied to *P* values of the pairwise associations in order to avoid this inflated probability.

Test of the chronosequence using a simulated dataset

We assessed the performance of the analytical approach by applying it to three different simulated repeated measurements' datasets with known predefined properties. This allowed us to provide background for contrasting and discussing our results from real data. Dataset simulation was done by setting a logistic chronosequence model and then generating random values from it, which constituted initial (chronosequence) observations for different sites. Simulated trajectories for each of these sites were then created based on the expected trajectory defined by the chronosequence model. We allowed for variation in one of three criteria: 1) sample size, 2) amount of random variation in site trajectories, and 3) degree of systematic departure of observed trajectories from those expected from the chronosequence model. Performance of the analytical approach was assessed as described before (see step 6 above). Further details on simulation and their results are shown in Appendix S2.2.

Results

Age of abandonment as an explanatory variable of community attributes and their observed changes

Chronosequence models showed that age of abandonment had a high explanatory power for all of the six attributes of the TDFs. Overall, age explained 60-97 % of the differences in community attributes across sites (Table 2.1a). Structural attributes, namely basal area, plant density and mean plant height, were better explained by age ($R^2 = 0.79-0.97$) than were species richness, evenness and species composition ($R^2 = 0.60-0.80$; Fig. 2.1; Table 2.1a). Basal area and plant density showed a sigmoid trajectory (Fig. 2.1A,B), while the other attributes exhibited a more asymptotic one (Fig. 2.1C-F).

Observed net changes in community attributes (NC_{obs}) were partially explained by age of abandonment (Table 2.1b). Age explained NC_{obs} better for species richness, evenness and composition ($R^2 = 0.53-0.57$) than for structural attributes ($R^2 = 0.06-0.40$). Net change models for basal area and plant density described a humped pattern in relation to age (Fig. 2.2A,B), while those of other attributes describe a negative trajectory (Fig. 2.2D-F). The NC_{obs} for mean plant height did not show any relation to age (Fig. 2.2C, Table 2.1b).

Table 2.1. Parameters and statistics for (a) chronosequence models testing the effects of age of abandonment on attribute inter-site variation and (b) net change models testing the effects of age of abandonment on recorded changes of community attributes of secondary tropical dry forest woody communities in abandoned pastures and old-growth forest sites in western Mexico. Chronosequence models were adjusted using 2004 data. Observed net changes in attributes correspond to the 2004 through 2010 period. Model refers to the form of the fitted model, with a, b, c, α , β , and γ being model parameters; see Table S1 for model and parameter definitions. RSE is residual standard error, and R^2 is coefficient of determination. Parameters in bold are those testing the effect of age of abandonment. Significance levels are ** $P < 0.01$ and * $P < 0.05$.

(a) Chronosequence models^a

Attribute	Model	a	b	c	RSE	R^2
Basal Area	Gompertz	21.24**	4.29**	0.80**	1.69	0.97
Plant density	Logistic	6044**	5.51**	2.38**	822	0.91
Height	Logistic	5.93**	-0.75	5.69**	0.616	0.79
Rarefied richness	Logistic	24.87**	1.16	4.44**	2.86	0.80
Evenness	Logistic	0.94**	-15.02**	6.89**	0.031	0.60
Composition	Logistic	1.39**	4.91*	5.11**	0.279	0.71

(b) Net change models^b

Observed change	Model	α	β	γ	RSE	R^2
Basal Area	Gompertz	38.12**	3.56**	0.56**	2.40	0.32
Plant density	Logistic	13320**	2.42	0.79**	1380	0.40
Height	Logistic	1.06	6.28**	1.09**	0.044	0.06
Rarefied richness	Logistic	95.4**	2.63	3.84**	2.27	0.57
Evenness (PIE)	Logistic	1.32*	-1.13	5.92*	0.002	0.53
Composition	Logistic	1.86**	5.56*	2.53**	0.081	0.53

^aModels fitted to community attributes were selected on the basis of minimization of AICc from four possibilities: Michaelis-Menten, Asymptotic, Gompertz, and Logistic. ^bModels fitted to observed net changes correspond to the first derivatives of selected chronosequence models.

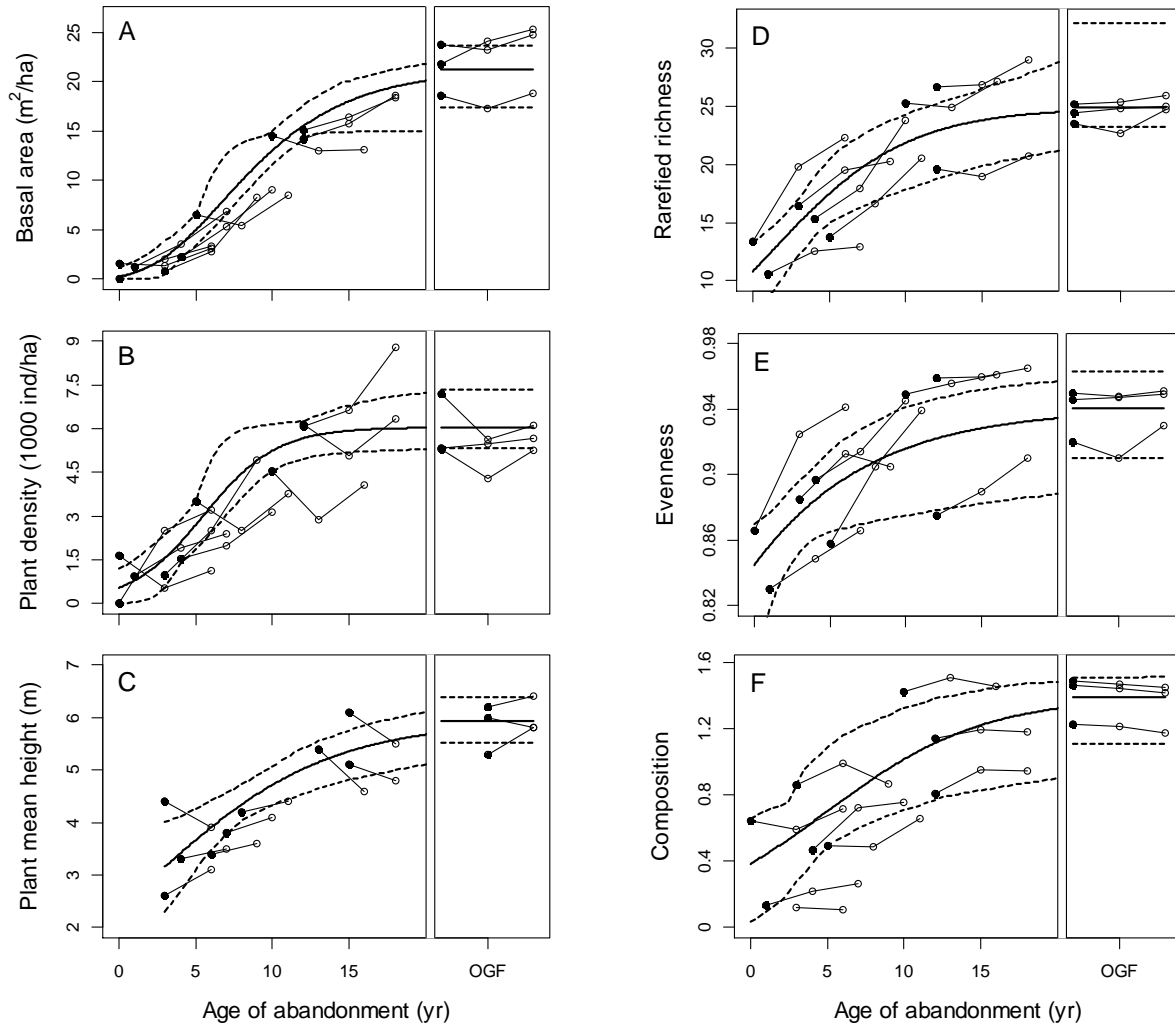


Figure 2.1. Woody community attributes as a function of age of abandonment of secondary TDF in the Chamela-Cuixmala region, western Mexico. Attribute values for the same site in different years are linked with solid thin lines. Black dots represent community values for 2004 (2007 for plant mean height), and white dots are values for 2007 and 2010. Black, continuous thick lines represent chronosequence models fitted to black dots (as in Table 1) and dotted lines their percentile-based, 95% CI limits. OGF refers to old-growth forest sites.

Chronosequence power for predicting observed attribute changes

Net change models for the woody communities in the TDFs described successional trajectories that fell consistently below the expected trajectories for basal area, plant density, mean height, and species composition (Fig. 2.2). On the contrary, the NC_{obs} trajectory for evenness was consistently above the expected one. Overestimation was significant for two structural attributes, basal area and mean plant height, as trajectories defined by their net change models fell outside confidence intervals of the NC_{exp} trajectories

(Fig. 2.2A,C). In contrast, chronosequence attribute models adequately predicted those NC_{obs} trajectories for two species based attributes: rarefied richness and species composition (Fig. 2.2D,F). NC_{obs} trajectories for plant density and species evenness fell partially inside the confidence interval (Fig. 2.2B,E).

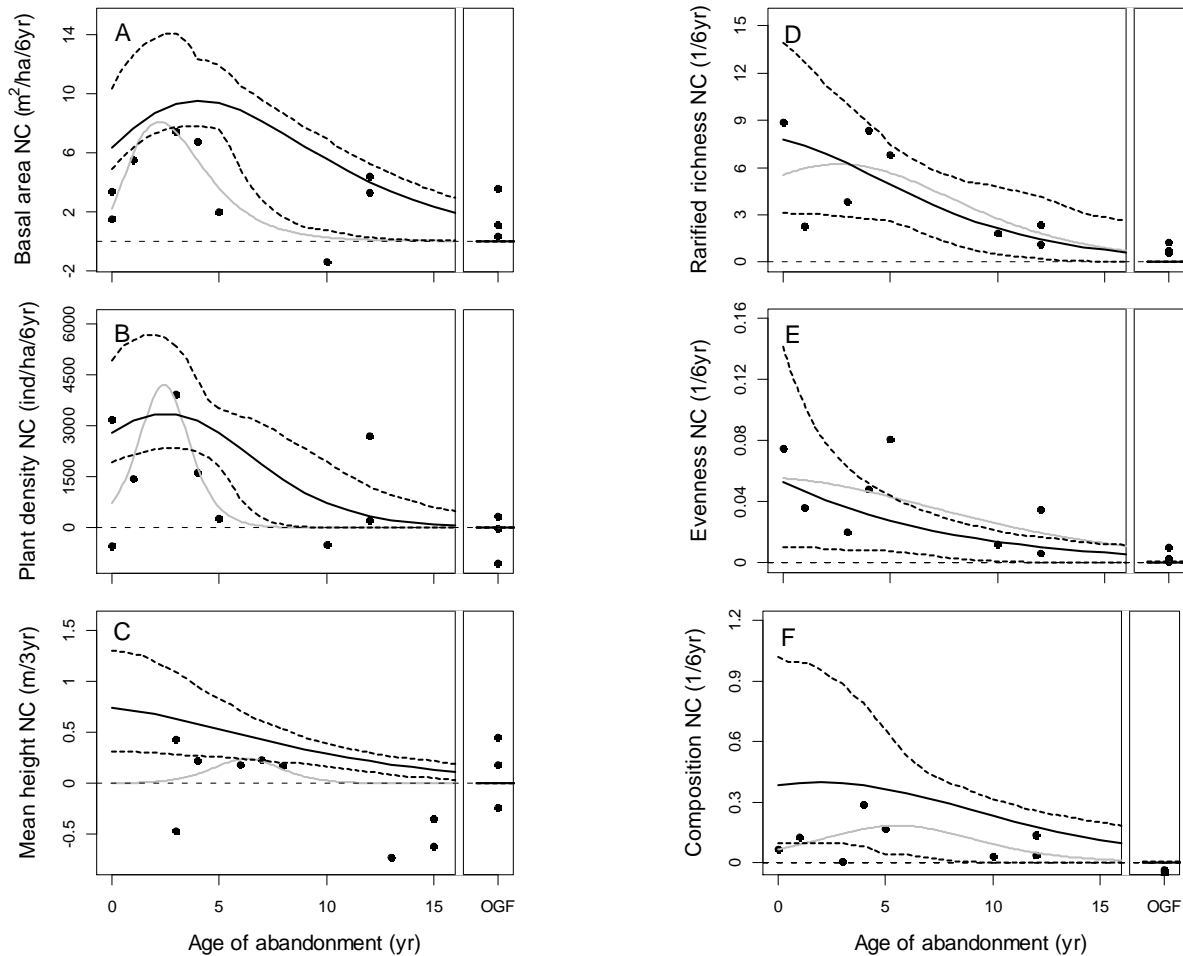


Figure 2.2. Net changes (NC) in community attributes as a function of age of abandonment of secondary tropical dry forests in the Chamela-Cuixmala region, western Mexico. Dots represent observed net changes for each site, calculated for the 2004 through 2010 period (2007-2010 for plant mean height). Gray continuous lines represent the net change models fitted to observed changes. Black continuous lines represent expected attribute changes from chronosequence models fitted to community attributes (see Fig. 1), with dotted lines being their 95 % CI limits. OGF refers to old-growth forest sites.

Site factors influencing succession

Ordination axes derived from site factors did not explain residuals from chronosequence models, but partially explained residuals from some net change models (Table 2.2). The residuals of the model for net changes in mean height were related to ordination axis-3 (Table 2.2), which in turn was linked to different aspects of forest clearing, cattle grazing regime, and extraction of timber (Table S2.2). Residuals of the models for net changes in species richness and composition were related to ordination axis-2 (Table 2.2), which was related to different aspects of field management, cattle activity, soil condition, and adjacent forest cover (Table S2.2). For these three net change model residuals, we found significant correlations with site variables associated with ordination axes-2 and 3 (Fig. 2.3). For mean plant height, residuals increased as years since last slash increased (Fig. 2.3A). Residuals from species richness decreased as the extension of forest clearing increased or when no herbicide was applied for weed control (Fig. 2.3B-C). Finally, residuals from species composition decreased as the duration of cattle grazing and timber extraction duration and extension increased (Fig. 2.3D-F). Adjacent forest cover variables did not show any significant association with residuals, although coverage in 200 and 300 m buffers were associated with axis-3 (Table S2.2). Adjacent forest cover variables were highly correlated with age of abandonment (Spearman rank correlation coefficients = 0.63 ($P < 0.01$), 0.70 ($P < 0.05$), 0.77 ($P < 0.05$) for buffer areas of 100, 200 and 300 m radius, respectively.

Table 2.2. Linear models testing for the effects of site factors on residuals from chronosequence models and net change models shown in Table 1. Only those residuals with significant effects are shown. Site variables assessing management history, soil condition, and adjacent forest cover (see Appendix S3) were reduced to three ordination axes (A1 to A3) which were further included in the models. The Coef i column refers to model parameter relating residuals and age of abandonment. RSE is residual standard error, R^2 is coefficient of determination and NC_{obs} are observed net changes. Significance codes** are ** $P < 0.01$ and * $P < 0.05$

Model residuals	Axis	Coef i	RSE	R^2
Height NC _{obs}	A-3	0.039*	0.051	0.44
Richness NC _{obs}	A-2	0.277*	0.273	0.58
Composition NC _{obs}	A-2	0.009*	0.010	0.51

Performance of the analytical approach using simulated datasets

Both the amount of random or systematic error in site trajectories caused significant and consistent divergence between observed and expected net changes (Fig. S2.2-2,3). Variation in sample size had less effect on divergence between chronosequence and dynamic

approaches, with small sample sizes sometimes leading to partial departure from chronosequence expectations (Fig. S2.2-1).

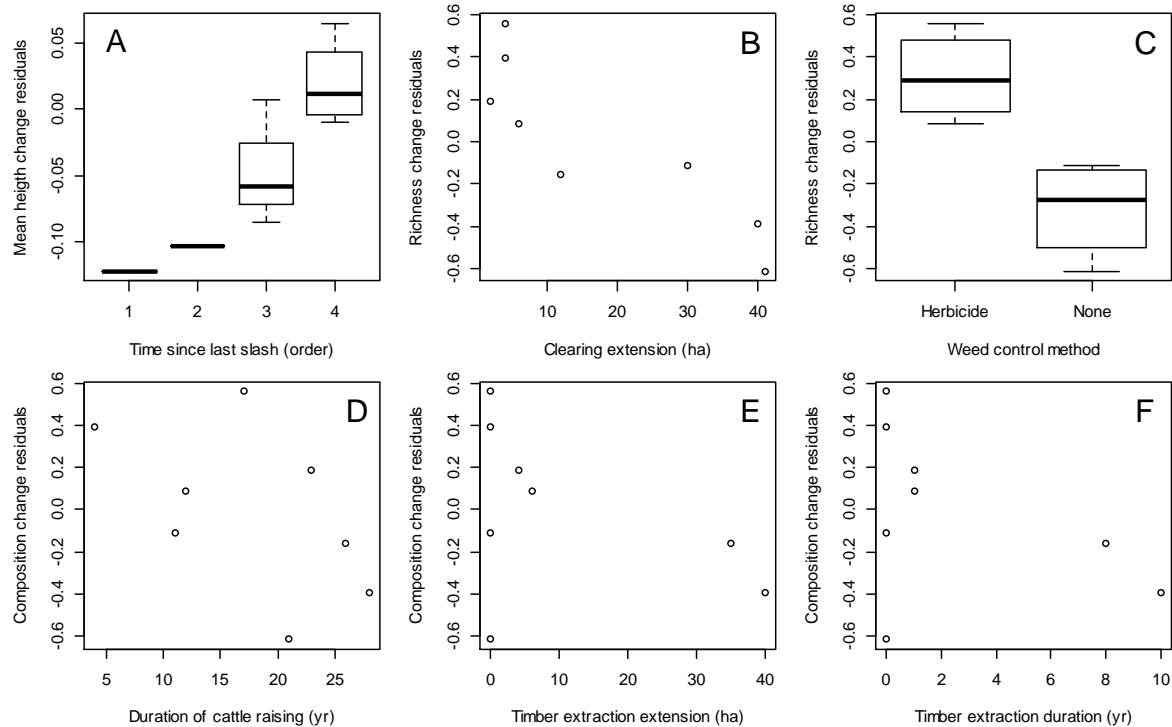


Figure 2.3. Pairwise relationships between residuals from chronosequence models or net change models and site variables assessing management history, soil condition and adjacent forest cover in secondary TDF from the Chamela-Cuixmala region, western Mexico. Only those residuals and site variables significantly associated with ordination axis explaining them are shown; $P < 0.05$, Bonferroni corrected Spearman rank correlation tests). See Table 2.2 and text for further details.

Discussion

Age of abandonment as explanatory variable of community attributes and their observed changes

Age of abandonment was clearly a major factor explaining variation in community attributes based on chronosequence data in secondary TDFs in Chamela. Similar results have been observed in other chronosequence-based studies where sites were selected with similar criteria, *i.e.*, seemingly homogeneous environmental and historic conditions (Peña-Claros, 2003; Chazdon, 2008; Vargas *et al.*, 2008; Lebrija-Trejos *et al.*, 2010a; Muñoz-Castro *et al.*, 2011). The explanatory power of age, however, varied with the attribute analyzed: it was higher for structural attributes than for diversity and composition. Structural attributes have

been shown to recover independently from the number or identity of species and to be less susceptible to deviation from the expected successional trajectory defined by age (Pascarella *et al.*, 2000; Molina Colón y Lugo, 2006; Marin-Spiotta *et al.*, 2007). Perhaps once a minimum set of species spanning over a range of functional responses is present, the recovery of forest structure proceeds in a more deterministic way, only loosely associated with the number or identity of species (Yachi y Loreau, 1999; Lasky *et al.*, 2014). The addition of new species seems necessary, though, to sustain forest recovery over time (Allan *et al.*, 2011).

Age of abandonment also explained variation in dynamic data, *i.e.*, observed attribute net changes across sites, but with lower explanatory power than for community attributes. Differences in explanatory power may be related to the effect of water availability at different time scales. Regarding rates of change, the study of the seedling community in the same chronosequence has shown that they are not related to age but rather to interannual variation in precipitation patterns (Maza-Villalobos *et al.*, 2011, 2013). In the case of community attributes, studies of the conserved forest show that they are clearly correlated to topographically driven differences in water availability (Lott *et al.*, 1987; Segura *et al.*, 2003). It then seems that while net changes in attributes may respond to short-term (interannual) water availability, which is highly variable and not related to age, community attributes could be representing the effect of historical average water availability captured by age of abandonment.

Match between observed and predicted changes in community attributes through time

Our results suggest that chronosequence models have less power to predict short-term successional dynamics for forest structural attributes than for species identity-based attributes like diversity or composition. The two attributes significantly and consistently overestimated by chronosequence models, namely basal area and mean plant height, are structural attributes. The third structural attribute (plant density) was also overestimated, although not significantly along all the age range evaluated. On the contrary, species-based attributes were not significantly over- or underestimated, although species evenness and composition net change models fell partially outside intervals predicted from chronosequences. These results contrast with the explanatory power of the chronosequence models, for which structural attributes like basal area and plant density had higher R^2 values, but did not perform better in predicting observed net changes than species-based models like evenness and composition with lower R^2 . Therefore, there seems to be no relation between R^2 values of the chronosequences and their predictive power.

These findings contradict the generalized view that chronosequence models predict changes of structural attributes, particularly basal area, better than those of diversity or taxonomic composition (Chazdon *et al.*, 2007; Quesada *et al.*, 2009). This view is mostly based on the commonly high R^2 values found for structural variables when using chronosequence approaches. Other studies, however, have also shown wide variation in the predictive power of the chronosequences with strong departures of the observed from the expected trajectories (van Breugel *et al.*, 2006; Chazdon *et al.*, 2007; Feldpausch *et al.*, 2007) as well as close matches (Foster y Tilman, 2000; Lebrija-Trejos *et al.*, 2010a). Therefore ours and other studies show that the power of chronosequence models to predict short-term dynamics in successional forest may be site- or even attribute-dependent and should not be deduced from their explanatory power.

The possibility of a mismatch between chronosequences and dynamic approaches has potential implications for the application of the chronosequence approach to practical situations. For example, biomass and carbon stock recovery through succession in tropical forests is commonly inferred from forest structural measurements done along a chronosequence (Vargas *et al.*, 2008; Yang *et al.*, 2011; Becknell *et al.*, 2012). As previously shown, however, net changes of structural attributes derived from chronosequences can be quite dissimilar from those observed through repeated measurements, making biomass and carbon recovery estimations significantly biased. Our findings therefore indicate the need for caution in the application of chronosequence data in evaluations of ecosystem service recovery.

Influence of site factors on succession

In our study, sites were selected to conform a chronosequence based on their location on similar biophysical conditions and to include the dominant field management features in the study region (Burgos y Maass, 2004). Our results show, however, that variation in community dynamics is related to site factors, mainly those associated with field management previous to abandonment, even after accounting for the effect of age of abandonment. Such results suggest that field management history affects successional processes. In general, the higher residuals from net change models were associated with low extension or duration of field management and time since forest clearing (Fig. 2.3). An exception to this pattern was the higher residuals of the net changes model for richness found in sites where herbicide was applied. Thus, our results are in general concordance with previous findings about reduced successional recovery under more severe field management (Uhl *et al.*, 1988; Moran *et al.*, 2000; Zarin *et al.*, 2005; Molina Colón y Lugo,

2006). An interesting implication of these results is the complexities involved in site selection for chronosequences: an assessment of management history is required to guarantee that sites have very similar management histories or, even better, that information is included during chronosequence data analysis. Further work is needed to more strongly support these findings by increasing sample size of plots and by including more contrasting field management conditions.

It is also interesting that both soil properties and adjacent forest cover did not show any association with the observed successional dynamics, although they were related to ordination axes-2 and 3. The limited contribution of soil conditions contrast with the sharp mosaic in geological origin found in the region (Cotler *et al.*, 2002). Our results, though, concur with previous studies that showed that old-growth TDF structure and diversity in the region is not affected by the type of geology and soil (Durán *et al.*, 2006), but rather by water availability, associated to the slope and position in the landscape (Balvanera *et al.*, 2002). The lack of association between adjacent forest cover and model residuals could be explained by inadequate sampling or by the correlation between adjacent forest cover and age of abandonment. Our sample was not designed to test the effect of the surrounding landscape matrix features on site dynamics, so the lack of association could simply be the result of inadequate representation of the complete range of forest coverage around sites. On the other hand, we also found a significant correlation between age and forest cover, which we speculate could result from the spatial autocorrelation of management practices (Helmer *et al.*, 2008; Crk *et al.*, 2009). This correlation could imply that when testing the effect of age of abandonment, we may not only have tested the intrinsic processes of development of the forest, *i.e.* plant growth, but also the potential effect of extrinsic factors like increased seed rain and seedling establishment associated with increased adjacent forest cover, as has been previously shown (Maza-Villalobos *et al.*, 2011).

Sample size limitations and performance of the analytical approach

Our conclusions could be limited by the small sample size of the tropical dry forest dataset (nine secondary forest sites). Results from the analysis of these data, however, are consistent with the performance of the analytical approach under simulated conditions. NC_{exp} trajectories observed for those community attributes with significant departure from expectations (basal area and mean height) are more consistent with a systematic departure of observed trajectories from chronosequence models than with a spurious effect caused by small sample size. Although small sample sizes caused a partial departure from chronosequence expectations during simulations, the analytical approach is relatively

robust to sample size. Instead of causing the spurious rejection of chronosequence expectations, small sample size seems to be related to the reduced power of the test, since prediction intervals become wider as sample size reduces. On the contrary, simulations testing the effect of the degree of systematic departure between observed and expected NC show the test is sensitive to this parameter. Increased random deviation also results in higher divergence between observed and expected results (Appendix S2.2). Overall, simulations suggest that the analytical approach is sensitive to deviation in successional trajectories with respect to chronosequence model expectations.

We believe the analytical approach developed here has clear advantages beyond low sensitivity to sample size. Previous studies have tested the match between chronosequence and dynamic approaches by correlating predicted rates from a chronosequence model to observed rates (Maza-Villalobos *et al.*, 2011). This constitutes a “coarse test” of the chronosequence, since correlation can occur even when observed and expected rates show a different kind of relationship with time and, therefore, come from quantitatively different relationships between age and community attributes. In addition, correlations between age and observed rates do not actually test chronosequence predictions, as exemplified here by basal area, where the NC_{obs} were significantly related to fallow age, but the chronosequence model failed to predict them (*e.g.* Foster y Tilman 2000). Instead, our approach allowed us to test for specific predictions about expected community changes derived from specific statistical models fitted to community attributes. Its implementation in other chronosequence datasets will allow further assessments of its advantages and shortcomings.

Conclusions

We found that although age of abandonment has a high explanatory power for differences in community attributes of secondary TDFs, the predictive power of chronosequence models can be poor and not related to its explanatory power. Part of the mismatch between observed and expected net community changes over 6 yr may be caused by temporal environmental conditions affecting short-term successional dynamics, although differences in management history among sites could also influence such disparity. Our results point out the need to integrate chronosequence and dynamic approaches to better understand and predict secondary succession; furthermore, they suggest that caution is needed when applying chronosequences to the evaluation of ecosystem services recovery. By providing an analytical approach to statistically test both the explanatory and predictive

power of chronosequences, we have advanced in the integration of different approaches to study succession and, therefore, in the recognition of their possibilities and limitations.

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Table S2.1. Nonlinear models used to test the effects of age of abandonment (t) on community attributes (z in chronosequence models) and their observed net changes ($\partial z/\partial t$) for secondary tropical dry forests in abandoned cattle pastures and old-growth forest sites in western Mexico. Net changes models are the first derivative in relation to age of abandonment of the corresponding chronosequence model.

Model name	Chronosequence model	Observed net changes model
Michaelis-Menten	$z = at/(b + t)$	$\partial z/\partial t = \alpha/(\beta + t) - at/(\beta + t)^2$
Asymptotic	$z = a + be^{-e^c t}$	$\partial z/\partial t = \beta e^{-2e^c t}$
Gompertz	$z = ae^{-bc^t}$	$\partial z/\partial t = -\alpha e^{-\beta \gamma^t} \beta \gamma^t \ln(\gamma)$
Logistic	$z = (a/(1 + e^{((b-t)/c)}))$	$\partial z/\partial t = (\alpha e^{((\beta-t)/\gamma)}/\gamma)/(1 + e^{((\beta-t)/\gamma)})^2$

Table S2.2. Site variables associated with ordination axes summarizing field management history, soil condition, and adjacent forest cover of secondary tropical dry forest woody communities in abandoned pastures in western Mexico. Values are squared Spearman correlation coefficients for continuous or ordinal site variable, or correlation ratios for categorical variables. Significance level are ** $P < 0.01$ and * $P < 0.05$.

Site Factor	Site Variable	Axis-1	Axis-2	Axis-3
Management	Time since first clearing	0.05	0.66**	0.20
	Tool used during clearing	0.02	0.35	0.50*
	Clearing extension (Ha)	0.20	0.52*	0.00
	Time since last clearing	0.00	0.46*	0.3
	Slashing for agriculture	0.04	0.02	0.56*
	Time since last slash	0.1	0.18	0.56*
	Agriculture	0.08	0.08	0.50*
	Agricultural cycle duration (mo)	0.03	0.20	0.55*
	Weed control method	0.34	0.43*	0.06
	Duration of cattle raising activity (yr)	0.03	0.65**	0.00
	Permanence of cattle in the plot during a year (mo)	0.00	0.03	0.57*
	Cattle density in the plot (heads/Ha)	0.71**	0.03	0.00
	Extension of cattle raising activity (Ha)	0.03	0.82**	0.02
	Time since last year of cattle raising (yr)	0.29	0.00	0.45*
	Time since grass introduction (yr)	0.02	0.77**	0.13
	Extension of seeding area for introduced pastures	0.03	0.82**	0.02
	Extension of slashing for pasture maintenance (Ha)	0.14	0.45*	0.01
	Extension of maintenance fire (Ha)	0.08	0.83**	0.00
	Timber extraction extension (Ha)	0.09	0.67**	0.07
Duration of timber extraction (yr)	0.10	0.73**	0.04	
Soil	Physiological depth (dm)	0.86**	0.00	0.00
	Available water capacity (L/m ²)	0.94**	0.00	0.00
	Field capacity (L/m ²)	0.94**	0.01	0.00
	Cation exchange capacity (eq/m ²)	0.81**	0.05	0.01
	Humus content (Kg/m ²)	0.82**	0.00	0.00
	Total nitrogen (Kg/m ²)	0.80**	0.00	0.00
	Available nitrogen (Kg/m ²)	0.80**	0.00	0.00
	Total Phosphorous (Kg/m ²)	0.80**	0.00	0.00

	Number of different types of erosion	0.76**	0.14	0.54*
	Soil erodibility (K)	0.09	0.25	0.75**
	Root density	0.24	0.59**	0.27
Forest Cover	Percentage of forest coverage at 200 m radius	0.01	0.03	0.47*
	Percentage of forest coverage at 300 m radius	0.00	0.03	0.58*

Appendix S2.1. Analytic procedure to explore the power of chronosequences to explain and predict successional changes based on repeated measurements.

The analytical approach used to test the power of age of abandonment and site factors to explain and predict succession proceeds through seven simple steps. Here we develop the approach and present an R code (in Courier font) to apply it to a simulated dataset, consisting of repeated measurements for a hypothetical forest attribute for 25 sites and separated by a time interval of 3 yr ($\Delta t = 3$). Three vectors are provided: `age.t1` (age of sites at first measurement) and `y.t1` and `y.t2`, the attribute values for first and second measurements, respectively. Fig. S2.1-1 depicts the observed trajectories for each site by linking repeated measurements with a line.

```
### The dataset ###
age.t1 <-
c(19,12,4,34,10,37,29,23,27,0,24,17,7,32,2,40,50,45,49,55,62,67,96,84,73)
y.t1 <-
c(31.4,24.0,1.1,64.8,35.6,79.9,74.7,43.9,50.0,0.1,48.8,34.6,33.8,61.0,12.4,73.2,90.8,82.8,85.1,102.8,115.2,112.9,92.4,87.7,73.9)
y.t2 <-
c(36.3,29.8,2.1,67.2,41.3,80.7,79.0,54.7,51.8,0.0,53.8,42.1,39.0,65.2,17.7,77.4,92.4,87.7,85.4,106.6,116.9,108.6,94.1,85.4,75.4)
```

Step 1. *Fitting a statistical model to the attribute data.* A statistical model is fitted to chronosequence data for a specific attribute ("chronosequence model") using data from the initial measurement on the chronosequence. Model fitting provides estimates of the parameters in the model. Based on those estimates the mean successional trajectory of the attribute is defined with the continuous line depicting the general tendency of the attribute in relation to time; see Fig. S1-1. Some common models are logarithmic, logistic or even humped (Peña-Claros, 2003; Vargas *et al.*, 2007). We do not elaborate here on statistical methods for selecting models, since these are described elsewhere (Crawley, 2007; Anderson, 2008). Hypothetical attribute data conform to a logistic model, so this model is fitted.

```
### Fit of the chronosequence model to the attribute data ###
chrono.model<-nls(y.t1~SSlogis(age.t1,a,b,c))
summary(chrono.model)
Formula: y.t1 ~ SSlogis(age.t1, a, b, c)

Parameters:
      Estimate Std. Error t value Pr(>|t|)
a    97.628      4.990   19.57 2.11e-15 ***
b    23.763      2.140   11.11 1.73e-10 ***
```

```

c 10.920      1.893      5.77 8.36e-06 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 10.92 on 22 degrees of freedom
Number of iterations to convergence: 0
Achieved convergence tolerance: 9.92e-06

### Plot of attribute values in relation to age ###
plot(age.t1,y.t1,type="p", pch=19, xlab="Age of abandonment (yr)",
      ylab="Forest attribute")
points(age.t1+3,y.t2)
for (i in 1:length(age.t1)) {
xs<-as.vector(c(age.t1[i],age.t1[i]+3))
ys<-as.vector(c(y.t1[i],y.t2[i]))
lines(xs,ys)
}

### Adding to the plot the mean successional trajectory from the
model fitted ###
timespan<-as.vector(seq(min(age.t1),max(age.t1),1))
y.model<-predict(chrono.model,list(age.t1 = timespan))
lines(timespan,y.model, lwd=2)

```

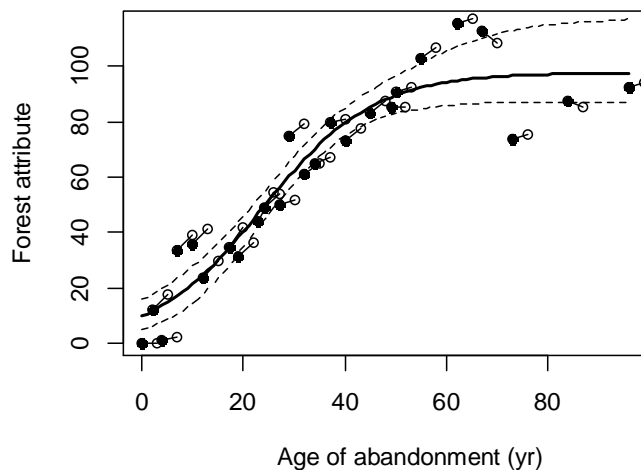


Figure S2.1-1. Chronosequence model and its 95 % CI for hypothetical data.

Step 2. *Calculating confidence intervals for the chronosequence model.* Confidence interval limits for the mean successional trajectory described by the chronosequence model are calculated using site bootstrapping (following Ritz y Streibig 2009). A site bootstrapping is performed 1000 times, so that each time a sample of size equal to the original sample (25 for our hypothetical sample) is obtained by sampling with replacement the original sample of sites. For each bootstrapped sample the chronosequence model is fitted and its mean successional trajectory established. Thus, a family of 1000 fitted models and their associated mean trajectories is established. Based on the set of 1000 trajectories, a percentile-based confidence interval for the mean successional trajectory is constructed. Fig. S1-1 depicts the 95 % CI for the chronosequences model of the hypothetical attribute (discontinuous lines).

```
### Fit of the model to bootstrapped samples ###
library(car)
B=1000 ### B defines number of bootstrap samples generated
modelboot.coef <- bootCase(chrono.model, B=B)

### Chronosequence model for each bootstrapped sample ###
alpha <- 0.05 # Here levels of significance can be set
predicted<-matrix(NA, B, length(timespan))
colnames(predicted)<-timespan
for(j in 1:B){
  params<-modelboot.coef[j,]
  for(k in 1:length(timespan)){
    predicted[j,k]<-params[1]/(1+exp(-(timespan[k]-
    params[2])/params[3]))
  }}

### Confidence intervals for chronosequence model ###
chrono.ci<-matrix(NA, length(timespan), 2)
for(k in 1:length(timespan)){
  chrono.ci[k,]<-as.vector(quantile(predicted[,k], c(alpha/2, 1-
  (alpha/2))))
}

### Adding to the plot the confidence intervals ###
lines(timespan,chrono.ci[,1], lwd=2, lty=2)
lines(timespan,chrono.ci[,2], lwd=2, lty=2)
```


Step 3. Calculating expected net changes in attributes. Community expected net changes in attribute (NC_{exp}) are calculated from the mean successional trajectory described by the chronosequence model. NC_{exp} were computed as the difference in the attribute values defined by the mean successional trajectory between the extremes of a time interval (Δt): $NC_{exp} = A_{t+\Delta t} - A_t$, along the whole age range (*i.e.*, for each possible value of age t). The time interval must match the time difference between subsequent repeated measurements ($\Delta t=3yr$ in our hypothetical dataset) in order to make observed and expected net changes comparable. Fig. S1-2 shows, as a continuous line, the mean expected net changes from the model fitted in step 1.

```
### Define time interval between subsequent measurements ###
delta.t<-3

### Defining expected net changes in attribute ###
timespan<-as.vector(seq(min(age.t1),max(age.t1),1))
y.model<-predict(chrono.model,list(age.t1 = timespan))
y.model.t1<-y.model[1:(length(y.model)-delta.t)]
y.model.t2<-y.model[(delta.t+1):length(y.model)]
NCexp<-y.model.t2-y.model.t1
```

Step 4. Calculating confidence intervals for expected net changes trajectory. We repeated step 3 but now for each of the mean trajectories calculated from bootstrapped samples in step 2. The result is a set of expected changes used to construct a percentile-based confidence interval for the expected attribute changes. Fig. S2.1-2 shows the confidence interval for expected attribute changes as discontinuous lines.

```
### Defining expected changes values from each bootstrapped sample
###
NCexp.boot<-matrix(NA, B, length(timespan)-delta.t)
colnames(NCexp.boot)<- timespan[1:(length(timespan)-delta.t)]
for (j in 1:B){
  for (k in 1:(length(timespan)-delta.t)) {
    NCexp.boot[j,k]<-(predicted[j,k+delta.t]-predicted[j,k])
  }
}

### Confidence intervals for mean expected net changes ###
NCexp.ci<-matrix(NA, (length(timespan)-delta.t), 2)
for(k in 1:ncol(NCexp.boot)){
```

```

NCexp.ci[k,]<-as.vector(quantile(NCexp.boot[,k],      c(alpha/2,      1-
(alpha/2))))
}

```

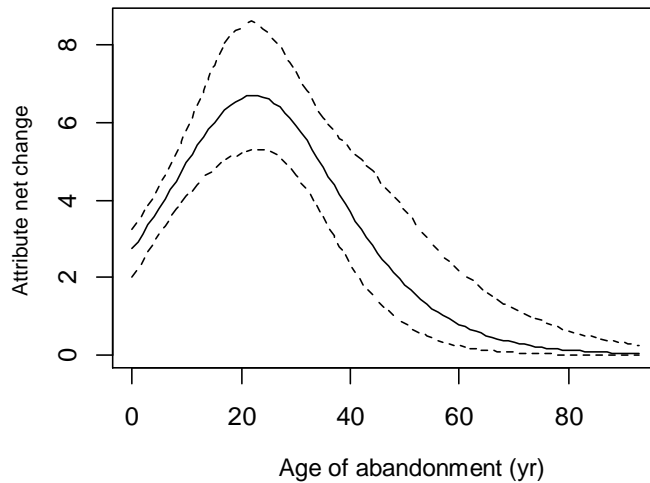


Figure S2.1-2. Expected net changes in attribute (NC_{exp} , continuous line) and their 95 % CI limits (discontinuous lines) in relation to age of abandonment.

Step 5. Fitting a statistical model to observed attribute net changes. Observed net changes through time (NC_{obs}) are calculated from repeated measurements by subtracting attribute values at the beginning of the time interval ($y.t1$) to the values at the end of it ($y.t2$). A statistical model relating NC_{obs} to age of abandonment is fitted (“net change model”). The function defining the relation between observed net changes in attribute and age of abandonment depends on the form of the chronosequence model fitted in Step 1. If site trajectories follow the expected attribute change trajectory derived from the chronosequence model, their associated observed changes should have a relation with age that follows a pattern described by the first derivative of the chronosequence model. Thus, fitting a statistical model of the form of the first derivative of the chronosequence model to the observed net changes should result in an adequate description of the relation between observed changes and age. Fig. S2.1-3 shows observed changes and the model fitted to them.

```

### Calculating observed net changes ###
NCobs<-y.t2-y.t1

### Derivative of the chronosequence model for attribute ###
logis<- expression(a/(1+exp((b-x)/c)))# logistic model as specified
in the SSlogis function in R
D(logis,name="x")
a * (exp((b - x)/c) * (1/c))/(1 + exp((b - x)/c))^2

```

```

### Fitting the derivative to the observed net changes ###
NCobs.model<- nls(NCobs ~ a*(exp((b-(age.t1))/c)*(1/c))/(1 + exp((b-
(age.t1))/c))^2,start=coef(chrono.model))
summary(NCobs.model)

Formula: delta.obs ~ a * (exp((b - (age.t1))/c) * (1/c))/(1 + exp((b -
- (age.t1))/c))^2

Parameters:
      Estimate Std. Error t value Pr(>|t|)
a  237.491      44.167    5.377 2.12e-05 ***
b   18.992       2.723    6.975 5.32e-07 ***
c    9.283       2.281    4.069 0.000509 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 2.385 on 22 degrees of freedom
Number of iterations to convergence: 13
Achieved convergence tolerance: 7.23e-06

```

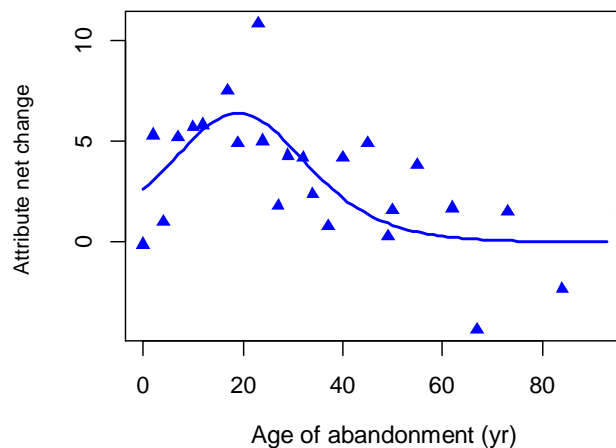


Figure S2.1-3. Observed attribute net changes (triangles) and the corresponding trajectory for the net change model (line).

Step 6. *Comparing expected and observed net changes.* The predictive power of the chronosequence model is tested by comparing the match between the model fitted to observed attribute net changes (step 5) and the mean and the confidence interval of the expected attribute net changes (steps 3 and 4). If the chronosequence model adequately predicts mean net changes through time, the model fitted to observed net changes should lie inside the confidence intervals for

the expected net changes. Otherwise, the model would be on average underestimating or overestimating the changes, at least for part of the age of abandonment timespan. Note that the test does not proceed through direct comparison of observed changes (each data) and the confidence interval, since it describes the region on which the mean trajectory for observed changes is expected to lie, rather than the individual observations.

Fig. S2.1- 4 compares observed and expected trajectories for our hypothetical data. In this case, the chronosequence model for attributes provides a good prediction of the mean trajectory for observed changes for age of abandonments between 0 and 20 yr; however, for ages > 20 yr, mean expected changes are higher than observed changes. In particular, for ages between 30 and 45 there are significant departures from the expected model.

```

plot(timespan[1:(length(timespan)-delta.t)], NCexp,type="l",
xlab="Age of abandonment (yr)", ylab="Attribute change",
ylim=c(min(NCobs,NCexp),max(NCobs,NCexp)))
lines(timespan[1:(length(timespan)-delta.t)], NCexp.ci[,1],
col="black", lty=2, lwd=1.5)
lines(timespan[1:(length(timespan)-delta.t)], NCexp.ci[,2],
col="black", lty=2, lwd=1.5)
points(age.t1, NCobs, pch=17, col="blue")
Xv<-timespan[1:(length(timespan)-delta.t)]
Yv<-predict(NCobs.model,list(age.t1=Xv))
lines(Xv,Yv,col="blue", lwd=2)

```

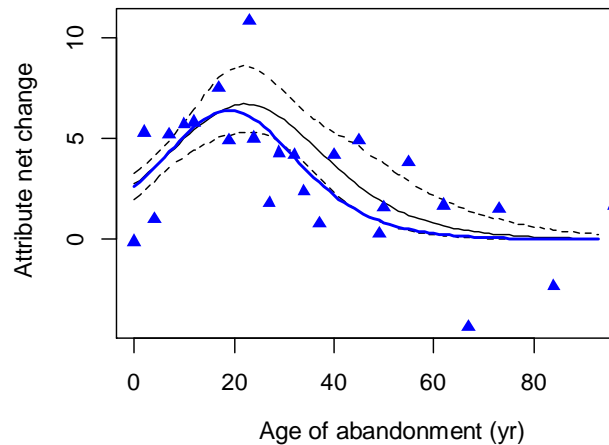


FIGURE S2.1-4. Comparison between expected net changes (NC_{exp}) predicted from chronosequence (the mean, a black continuous line and the confidence interval, a dotted line) and those observed (NC_{obs} , triangles and blue line) from dynamic data.

Step 7. *Site factors as explanatory variables of the among site variation in community attributes and their observed net changes.* To test if site factors beyond site age explain observed attributes or their observed changes, residuals from the chronosequence model (step 1) and the net change model (step 5) are related to additional site factors using other statistical models.

```
res.attrib <- residuals(model)
model.resid.attr<-lm(res.attrib~Axis1+Axis2+Axis3)
summary(model.resid.attr)
```

Appendix S2.2. Simulations for assessing the performance of the analytical approach to test chronosequence predictions based on the repeated measurements data.

In order to assess the performance of the approach for testing chronosequence models, simulated datasets were generated and the approach implemented. We assessed effects of sample size, amount of random variation in observed changes, and departure of observed changes from expected changes.

First, a baseline dataset with forest age and forest attribute values was simulated using a logistic function to relate both variables:

$$\text{attribute} = a / (1 + \exp((b - \text{age}) / c)) + \text{error}$$

Parameter values were set as $a = 100$, $b = 20$ and $c = 15$ for a baseline dataset. Age varied from 0 to 100 yr. Error was set as a normal random variable with mean and standard deviation equal to 0 and 10, respectively. Sample size was 25 sites. Observed changes were simulated by fitting the model to the attribute data, calculating the expected changes from it (setting $\Delta t = 3$), and then adding a random error from a normal distribution with 0 and 1 as mean and standard deviation, respectively.

Variations from this base scenario were then simulated as described below.

- 1) *Sample size*. Four datasets that differed in the number of sites (13, 25 as in the baseline, 50 and 100) were generated and analyzed. Each smaller sample was a subset of the bigger samples.
- 2) *Degree of random variation*. Four datasets that differed in the degree of variation in the observed attribute changes were generated by changing the standard deviation of the random term added to the expected values ($sd = 1$ as in the baseline, 2, 4, and 8).
- 3) *Degree of systematic departure of observed changes from expected changes*. Four datasets that varied in the magnitude of systematic departure between observed and expected changes were generated by multiplying expected changes by a factor of 0.5, 1 (baseline), 2, and 4. A random error term was then added (as defined for the baseline scenario).

The analytic procedure to explore the power of chronosequences to explain and predict successional changes was then implemented (steps 1 through 6); see the methods section and Appendix S1). Although simulated datasets can vary each time they are generated (as a result of random errors), results did not vary qualitatively from time to time, and thus we present the results for only one set of simulations. For each of the variations evaluated, the chronosequence model for the attribute was plotted to graphically compare expected changes and observed changes.

1. Sample size. As sample size decreases the trajectory for observed changes tends to differ more from the expected changes trajectory; however, the amplitude of the confidence interval for expected attribute changes also tends to increase as sample size decreases. As a result, most of the observed trajectory falls within the confidence interval of the expected trajectory even for the smallest sample size. Further simulations based on different baseline datasets (not shown) reveal that decreased sample size is not necessarily related to increased departure of observed trajectory from expected trajectory.

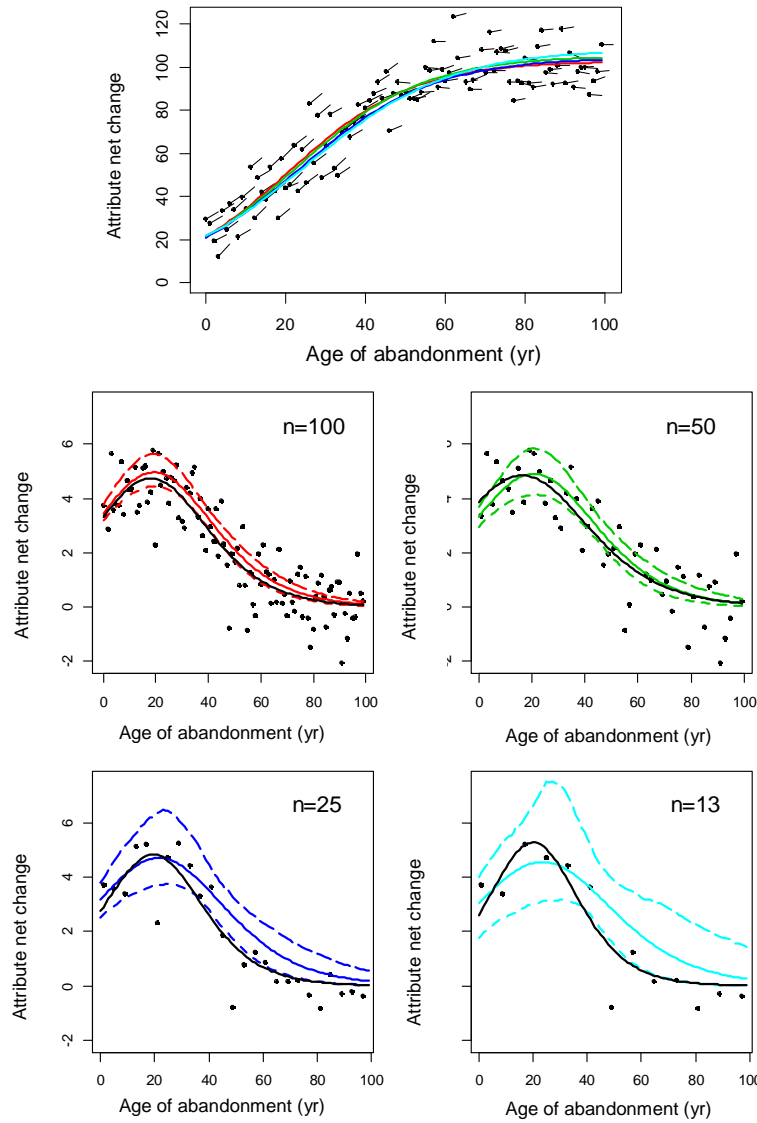


Figure S2.2-1. Simulation results for sample size variation. The panel on the top depicts the attribute data, with black points being the attribute data for the first measurement and small lines describing site trajectories derived from repeated measurements. Continuous lines in colors depict the chronosequence models fitted to each of the four sample sizes tested. The four bottom panels present the comparisons between observed (in black) and expected (in colors) trajectories for net changes in the attribute for each sample size (n).

2. Amount of random variation. As randomness increases (increased standard deviation associated with the observed changes), observed trajectory tends to differ more from the expected trajectory. In this case, departure is associated with an increased probability of the observed changes' trajectory falling outside the confidence interval for the expected changes' trajectory. Further simulations based on different baseline data (not shown) reveal that this result was consistent throughout the different simulations.

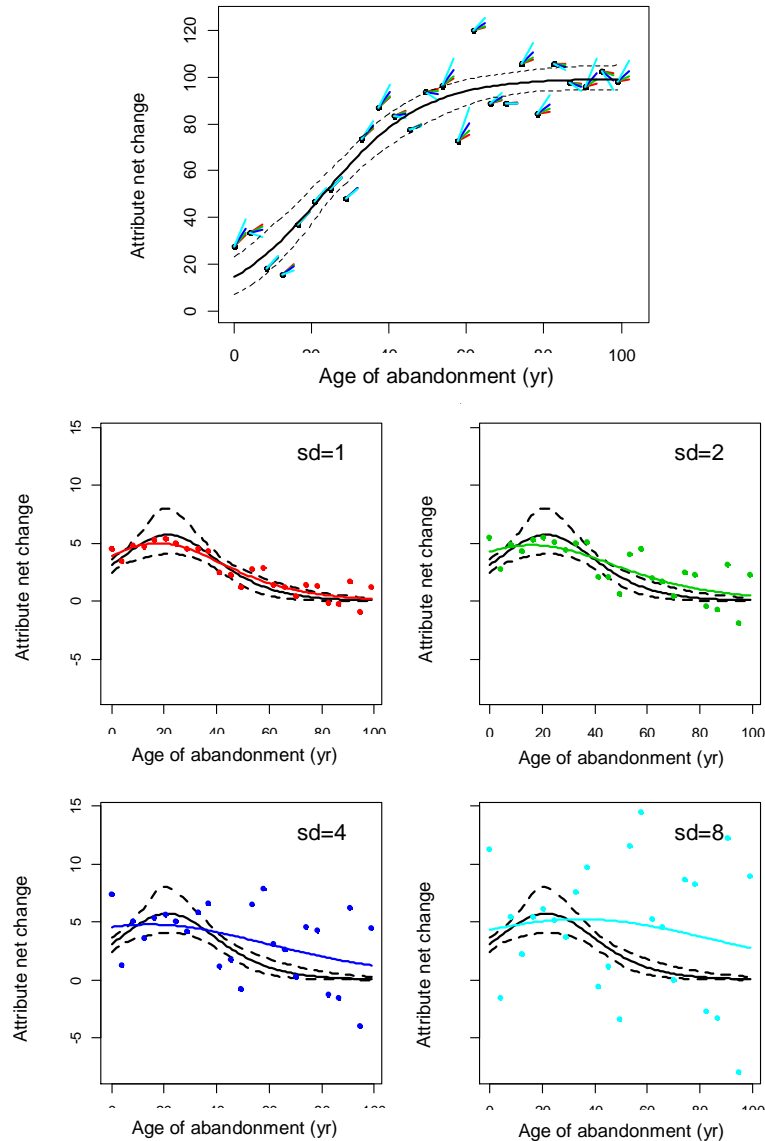


Figure S2.2-2. Simulation results for variation in randomness of observed changes. The panel on the top depicts as points the attribute data for the first measurement. Lines departing from points are site trajectories through the 3 yr period for the four different level of random variation. The four bottom panels present the comparisons between observed (in colors) and expected (in black) trajectories for attribute changes for each level of randomness. The standard deviation (sd) of the random normal term used to generate randomness in observed changes is indicated.

3. Degree of systematic departure from expected changes. No systematic bias in observed changes (factor = 1) generates an observed trajectory that match the expected trajectory. On the contrary, systematic underestimation (factor = 0.5) or overestimation (factor > 1) leads to significant departures of the observed trajectory from the confidence interval for the expected trajectory. Further simulations based on different baseline data (not shown) reveal that this pattern was consistent.

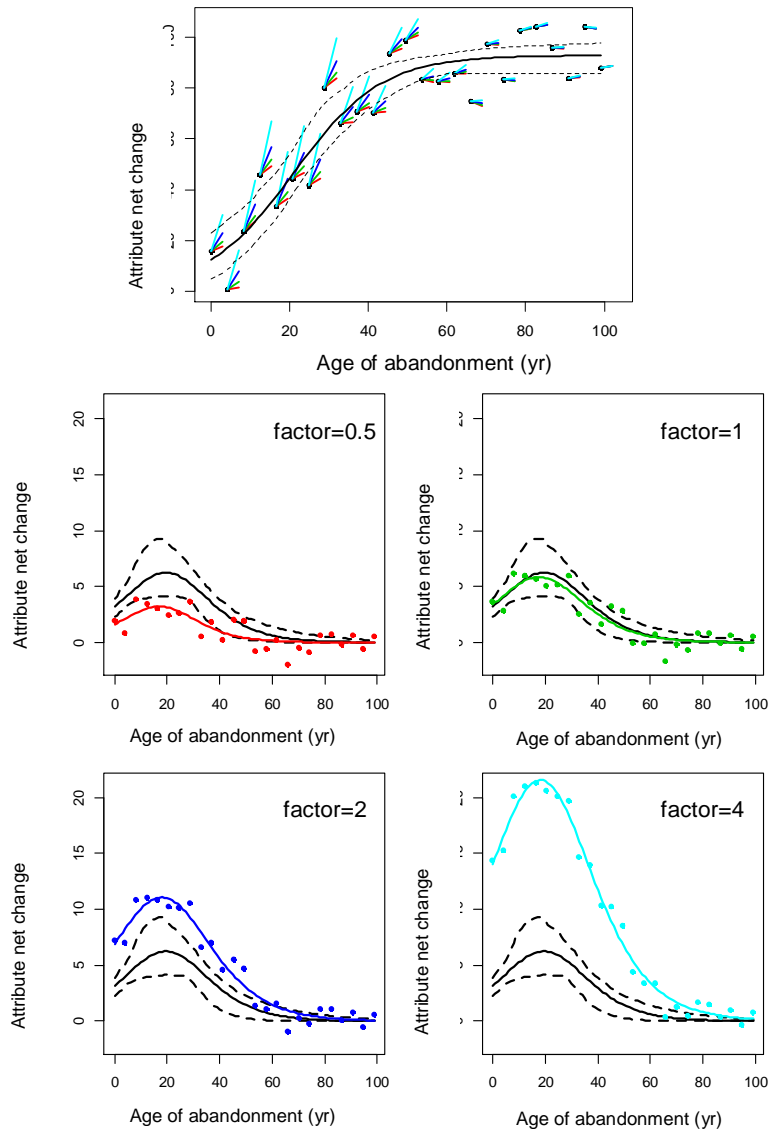


Figure S2.2-3. Simulation results for variation in the degree of systematic departure between observed changes and expected changes. The panel on the top depicts as points the attribute data for the first measurement. Lines departing from points are site trajectories through the 3 yr period for the four different levels of systematic departure of observed changes from expected ones. The four bottom panels present the comparisons between observed (in black) and expected (in colors) mean trajectories for attribute changes for each degree of systematic departure. Departure was included as a multiplier factor for the expected changes used to calculate observed changes, with factor = 1 as a no departure scenario, factor < 1 a systematic underestimation, and factor > 1 a systematic overestimation.

Appendix S2.3. Site factors beyond age of abandonment explaining community attributes and observed net changes.

Management history. Management previous to plot settlement was characterized through semi-structured interviews with landowners (Trilleras, 2008), and summarized in 43 variables related to frequency, magnitude, intensity and duration of agricultural, pastoral and extractive activities .

Variable	Type
Time since first clearing	Quantitative
Tool used during clearing	Categorical
Clearing extension (Ha)	Quantitative
Number of clearings	Quantitative
Time since last clearing	Quantitative
Slashing for agriculture	Categorical
Slashing extension (Ha)	Quantitative
Time since last slash	Ordinal
Agriculture	Categorical
Agricultural cycle duration (mo)	Quantitative
Number of agriculture events	Quantitative
Farming extension (Ha)	Quantitative
Number of weed controls	Quantitative
Weed control method	Categorical
Duration of weeding practice (yr)	Quantitative
Cattle density (heads/Ha)	Quantitative
Duration of cattle raising activity (yr)	Quantitative
Permanence of cattle in the plot during a year (mo)	Quantitative
Cattle density in the plot (heads/ha)	Quantitative
Extension of cattle raising activity (Ha)	Quantitative
Time since last year of cattle raising (yr)	Quantitative
Introduced grass species as forage	Categorical
Time since grass introduction (yr)	Quantitative
Use of herbicide for pasture maintenance	Categorical
Extension of introduced pasture's seeding area	Quantitative
Slashing for pasture maintenance	Categorical

Extension of slashing for pasture maintenance (Ha)	Quantitative
Times slashing was repeated	Quantitative
Duration of slashing activities for pasture maintenance (yr)	Quantitative
Use of fire for pasture maintenance	Categorical
Time since first burning	Ordinal
Extension of maintenance fire (Ha)	Quantitative
Times plot was burned	Quantitative
Times since last burning	Quantitative
Firewood extraction	Categorical
Firewood extraction extension (Ha)	Quantitative
Duration of firewood extraction (yr)	Quantitative
Timber extraction	Categorical
Timber extraction extension (Ha)	Quantitative
Duration of timber extraction (yr)	Quantitative
Stake extraction	Categorical
Stake extraction extension (Ha)	Quantitative
Duration of stake extraction (yr)	Quantitative

Soil condition. Soil ecological condition was assessed from 17 variables, including physical and chemical soil properties and soil degradation status (Table S2; Trilleras 2008). Soil data were gathered in 2006 from one soil profile in each site following criteria by Siebe *et al.* (2006). The variables measured and the methods used are shown below.

Variable	Type	Method used (following Siebe et al 2006)
Physiological depth (dm)	Quantitative	Direct observation
Total pore space (volumetric %)	Quantitative	Calculated from soil texture and soil bulk density (both measured in the field)
Aeration capacity (volumetric %)	Quantitative	Same as Total pore space
Available water capacity (L/m ²)	Quantitative	Same as Total pore space
Field capacity (L/m ²)	Quantitative	Same as Total pore space
Soil erodibility by water	Quantitative	Estimated using a nomogram
Cation exchange capacity (eq/m ²)	Quantitative	Calculated from soil texture, type of parent material and pH
Humus content (Kg/m ²)	Quantitative	Direct observation

Total nitrogen (Kg/m ²)	Quantitative	Estimated from type of humic material, bulk density, organic matter content, gravel content and horizon thickness
Available nitrogen (Kg/m ²)	Quantitative	Same as Total nitrogen
Total Phosphorous (Kg/m ²)	Quantitative	Same as Total nitrogen
Number of different types of erosion	Ordinal	Direct observation
Stability of soil aggregates	Ordinal	Field test for stable aggregates in water
Soil erodibility K	Ordinal	Estimated using a nomogram
Soil structure	Ordinal	Field observation
Root density	Ordinal	Root counts by dm ² for each horizon
Organic matter content	Ordinal	Estimated using a nomogram

Adjacent forest cover was quantified using 2003 true color imagery downloaded from Google Earth® and interpreted using ArcMap®. A supervised classification was done by differentiating two land cover categories, forested and not forested. Forested category included areas of at least 20 x 20 m with a continuous green to dark green coloration. It included strips of forest along streams, properties' boundaries, or live fences. No attempt was done to differentiate successional from old-growth forest. Non-forested category includes light green or brown areas, corresponding to open crops and pastures; isolated trees or patches of forest less than 20 x 20m were also included. Classification was done for three different buffer areas: 100 m, 200 m and 300 m. No further distance from plots was considered since forest cover percentage did not differ between the two largest buffer sizes and because seed dispersal for wind-dispersed seeds occurs mostly at short distances (Contreras-Sánchez *et al.*, 2011).

Variable	Type
Percentage of forest coverage at 100 m radius	Quantitative
Percentage of forest coverage at 200 m radius	Quantitative
Percentage of forest coverage at 300 m radius	Quantitative

Capítulo 3. *Changes in carbon stocks along tropical dry forest succession: Explanatory and predictive ability of forest age, tree diversity and chronosequence models*

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Submitted

Abstract

Although tropical secondary forests are considered important atmospheric carbon sinks, great uncertainty exists concerning estimates of their carbon (C) stocks, accumulation rates, and the drivers of their dynamics, particularly for tropical dry forests (TDF). We evaluated how C pools change along succession in a TDF in Mexico and assessed the role of forest age and tree diversity as drivers and predictors of C stocks and stock changes. Chronosequence trends in four C pools (aboveground biomass, surface litter, roots and top 10 cm soil) were tested using nonlinear models. Changes in aboveground biomass C stock predicted by the chronosequence model were compared with values observed after repeated measurements of the chronosequence. Causal relations among forest age, species and trait diversity with aboveground biomass C stocks and stock changes were tested using structural equation models. Total C stocks varied from 30.5 to 84.7 Mg C ha⁻¹. Aboveground, surface litter and root (< 20 mm diameter) C stocks increased asymptotically with forest age, whereas soil and large-root C did not. Observed stock changes in aboveground biomass ranged between -1.33 and 7.14 Mg C ha⁻¹ 3 yr⁻¹, and were not related to forest age, nor predicted by the chronosequence models. Aboveground tree biomass C was explained by forest age and the community weighted mean of species maximum tree height. Observed stock changes were related to both stock size and maximum tree height, although not consistently along the study period. Species diversity showed no additional explanatory power. Our results show that C accumulation in aboveground biomass along tropical dry forest succession is favored by the presence of high statured tree species, with the effect of this trait probably being emphasized in dry years, and suggest that chronosequences, widely used as a proxy to estimate both C stocks and rates of C uptake along succession, may overestimate their role as C sinks.

Introduction

Secondary forests are expected to play an increasing role in the global C cycle because of their growing representation across tropical landscapes (Wright, 2005, 2010). C uptake associated with forest regrowth during succession partially offsets gross C emissions from tropical regions (Defries *et al.*, 2002; Houghton, 2003; Achard, 2004). However, the magnitude of this effect is largely uncertain, with estimates from 5 to 20 % of emissions, or even up to 50 % when regrowth after both deforestation and logging is included (Pan *et al.*, 2011; Grace *et al.*, 2014). Uncertainty is partially driven by poor characterization of C uptake along succession (Houghton, 2003; Wright, 2010; Pan *et al.*, 2011), so improved quantification of C stocks in secondary forests and their change through time are needed to balance the global C budget (Houghton, 2003; Grace *et al.*, 2014).

Improved estimates of C stocks and their dynamics are particularly needed for tropical dry forest (TDF). Tropical dry regions comprise around 40 % of the tropical area worldwide and are undergoing significant deforestation and reforestation after land abandonment (Murphy y Lugo, 1986; Miles *et al.*, 2006; Aide *et al.*, 2013). However, scientific research on C in secondary forests has largely focused on tropical moist or rain forest ecosystems (Kauffman *et al.*, 2009; Jaramillo *et al.*, 2011; Meister *et al.*, 2012). Studies in secondary TDFs have documented aboveground biomass change with time since disturbance (Marin-Spiotta *et al.*, 2008; Becknell *et al.*, 2012; Martin *et al.*, 2013), but other C pools, such as dead aboveground biomass, roots or soil C have been poorly described (Jaramillo *et al.*, 2011). These pools are expected to be at least partially correlated because of allometric relations among plant parts (Niklas, 2004) and functional relations among pools (De Deyn *et al.*, 2008; Malhi, 2012). If quantified, the nature of the correlations among C pools could provide indirect estimates of those pools based on more readily available aboveground biomass measurements (Mokany *et al.*, 2006).

Time is considered the main driver of change in C stocks along forest succession and thus a relevant proxy for stock estimation. After disturbance, as succession proceeds, C is expected to accumulate in the ecosystem until an asymptote is reached, due to the added contributions of net primary productivity, tree mortality, and soil respiration (Chapin III *et al.*, 2011). Chronosequence studies, in which stocks are estimated across sites with different times since disturbance (commonly after land abandonment from agricultural use), have confirmed this accumulation pattern in aboveground biomass (Marin-Spiotta *et al.*, 2008; Becknell *et al.*, 2012; Martin *et al.*, 2013), although not in soil (Marin-Spiotta y Sharma, 2013). Decreasing rates of ecosystem C accumulation along succession have been inferred from such a chronosequence pattern (Vargas *et al.*, 2008; Yang *et al.*, 2011; Orihuela-Belmonte *et al.*, 2013). However, the use of the chronosequence approach to estimate C

stocks and to predict C accumulation rates can be questioned. The explanatory power of forest age on C stocks across secondary forests within a region, as measured by R^2 values from chronosequence models, is highly variable (Vargas *et al.*, 2008; Hernández-Stefanoni *et al.*, 2010; Orihuela-Belmonte *et al.*, 2013), therefore, the accuracy of estimations can be low. Also, it would be expected chronosequences to match observed trajectories of change derived from repeated measurements of successional forests, if forest age was a good predictor of C stock changes along succession. Available evidence suggests that such match is not necessarily true (Chazdon *et al.*, 2007; Feldpausch *et al.*, 2007) and that additional drivers of C accumulation during succession in tropical forests exist (Chazdon, 2008; Hernández-Stefanoni *et al.*, 2010; Orihuela-Belmonte *et al.*, 2013). Thus, a critical assessment of forest age as a predictor for C stocks and accumulation rates through succession is still needed.

Plant diversity is also expected to be a relevant driver of C stocks and C accumulation in the ecosystem. A general positive effect of plant richness on primary production and biomass of primary producers under experimentally controlled conditions has been shown (Cardinale *et al.*, 2011), but evidence from tropical forests remains equivocal. Under field conditions, tree species richness, functional diversity, and species functional traits correlate with aboveground C stocks and accumulation rates at a range of spatial scales (Erskine *et al.*, 2006; Chisholm *et al.*, 2013; Conti y Díaz, 2013; Lasky *et al.*, 2014; Finegan *et al.*, 2015). Soil C fluxes are also partially driven by plant traits (De Deyn *et al.*, 2008). However, tree diversity co-varies with forest age (Chazdon, 2008; Lohbeck *et al.*, 2013; Martin *et al.*, 2013), and likely, the variation in biomass or productivity is a consequence of the direct effect of age on forest structure (Lohbeck *et al.*, 2015b). Studies on the effects of both forest age and either species or functional tree diversity on C stocks are scarce (Barrufol *et al.*, 2013) and are needed to establish if biodiversity enhances C storage and sequestration in species-rich tropical forests (Díaz *et al.*, 2009). If so, it would provide stronger support for the explicit inclusion of biodiversity into climate change mitigation mechanisms (Harvey *et al.*, 2010; Paoli *et al.*, 2010).

In this study, we evaluate how different C pools change along succession in a TDF in western Mexico and we test the explanatory and predictive power of both forest age and tree diversity on C stocks and stock changes through time. We use a chronosequence approach to provide estimates of C stocks in four different ecosystem pools (aboveground biomass, surface litter, roots, and soil) across forests in different successional status, and to test how those stocks change along succession in relation to age and to other C pools. We then combine the chronosequence approach with a dynamic approach (repeated measurements during two consecutive 3-year periods, from 2004 to 2010) to assess C stock

changes in aboveground biomass through time and to test if they can be predicted from the chronosequence approach. Finally, we construct a model to assess causal relations among age, species plant diversity, functional attributes, aboveground biomass C stocks and stock changes over time through exploratory path analysis. Our main questions were: 1) What is the magnitude of C pools in secondary forests and how does it relate to forest age? 2) To what extent is the recovery of different C pools associated along succession? 3) Does a chronosequence model adequately predict C stock changes in aboveground biomass at the plot level? 4) Do different measures of diversity account for differences in C stocks and stock changes during succession after accounting for forest age?

Materials and methods

Study area and site characteristics

The study was conducted in the Chamela-Cuixmala Biosphere Reserve and adjacent areas, on the Pacific coast of the state of Jalisco, Mexico (19°23′ - 19°30′N, 104°56′ - 105°04′W). Mean annual temperature is 24.6°C. Mean annual precipitation over the period 1983-2013 is 756 mm, concentrated between June and October (data from the "Watershed Project", UNAM). The predominant land cover is TDF, but at least 16 % of the land adjacent to the reserve has been transformed during the past 40 years (Sánchez-Azofeifa *et al.*, 2009), mainly to pastures for livestock grazing. Those pastures are maintained through periodical slashing of the woody vegetation and burning. However, because of reduced productivity or change in country-level socioeconomic conditions, pasture management practices can be reduced or suppressed, which results in the development of secondary vegetation in this areas (Burgos y Maass, 2004).

Twelve sites (nine secondary forests developed from abandoned pastures and three old-growth forest sites without evidence of recent human disturbance) were selected to represent variation in age and stand structure of TDF across the region. The sites are part of a long-term project on forest succession (Martínez-Ramos *et al.*, 2012). The pastures had been abandoned for 0 to 12 years when the study began in November 2004, as determined through semi-structured interviews with landowners (Trilleras, 2008). All sites were located on South (Southeast to Southwest) facing slopes (15° to 30°) in hilly areas to control as much as possible for preexisting differences in water availability and soil type. Secondary forests were located in sites where land had been mainly used for cattle production during 4 to 28 years after slashing and burning of the original forest, with repeated burning,

planting of exotic grasses and free grazing. All secondary forest sites were fenced with barbed wire in 2004.

Carbon pools

C stocks on each site were assessed within four pools: aboveground live biomass carbon (ABC), surface litter carbon (LC), root carbon (RC) and soil carbon (SC). ABC was further subdivided into tree (ABC_T) and herbaceous (ABC_H) pools.

Aboveground live biomass C in trees. ABC_T was defined as the C stored in woody live trunks and stems of trees and shrubs above the soil surface (hereafter referred as trees). ABC_T was estimated from measuring all live woody stems ≥ 1 cm diameter at breast height (DBH) within a 20 \times 50 m plot at each site, following a stratified sampling approach (Figure S3.1): stems < 2.5 cm DBH were measured in half of the plot (10 \times 50 m area), whereas stems ≥ 2.5 cm DBH were measured in the whole plot. Measurements were taken between September and October 2010. Aboveground live woody biomass was estimated with a local allometric equation including DBH and wood density as predictors (Martínez-Yrizar *et al.*, 1992). Wood density values were obtained from published and unpublished data for the species at Chamela (Barajas-Morales, 1985, 1987; Martínez-Yrizar *et al.*, 1992). When site data were not available, species values from other locations or mean genus values were used (Chave *et al.*, 2006). For those species with no available information, a mean community value was assigned. Biomass C stocks were estimated by multiplying biomass by a conversion factor of 0.48 (Jaramillo *et al.*, 2003a). Lianas and cacti were not included in ABC estimates because of the lack of allometric equations for these life forms in TDF; however, they account for only 1.9 and 4.0 % of the basal area across all sites, respectively.

Aboveground biomass C in herbs and grasses. ABC_H was quantified by harvesting all the living material at ground level < 1 cm DBH in three 2 \times 0.5 m plots located 2 m away from the 20 \times 50 m plot (Figure S3.1). Biomass was harvested between March and April 2011. At this time most of the plants had no leaves with the exception of grasses. Thus, leaves from dicots were included in the litter component. Material was oven dried at 80°C to constant weight and weighed. Herbaceous biomass C stocks were estimated by multiplying biomass by a conversion factor of 0.46 (Jaramillo *et al.*, 2003a).

Root C. RC was defined as the C content in both live and dead roots. We excavated trenches in the same three 2 \times 0.5 m plots used for ABC_H estimation, between March and April 2011 (Figure S3.1), to a depth of 40 cm, because 80 to 88 % of the root biomass is found within this depth in pastures and forests of this region (Jaramillo *et al.*, 2003a). Soil was passed

through a 4 mm mesh to extract roots in the field. Roots were taken to the lab, washed with tap water and separated by hand in three diameter classes: small (< 4 mm), medium (4-20 mm), and large (>20 mm). Roots were oven-dried at 80°C to constant weight. Root C stocks were estimated by multiplying biomass by mean C concentrations by diameter class (Jaramillo *et al.*, 2003a).

Surface litter carbon. LC was defined as the C content in dead plant material lying above the surface of the mineral soil layer and, which was collected in nine 30 × 30 cm microplots at each site in April 2011. Three microplots were randomly located in the upper, middle and lower positions of the 10 × 50 m plot used for measuring trees > 1.0 cm DBH (Figure S3.1). The plant material was sieved through a 0.25 mm mesh to exclude mineral soil particles and then subdivided into three components: leaves, stems (true stems of all diameters plus detached petioles or rachis from compound leaves), and reproductive material (inflorescences, flowers, fruits and seeds). The samples were oven dried at 80°C to constant weight. LC stocks were estimated by multiplying biomass by conversion factors of 0.40 for leaves and reproductive material, and 0.49 for stems (Jaramillo *et al.*, 2003a).

Soil carbon. SC was defined as the total C content in the soil mineral layer to a 10 cm depth. In September 2009, three soil cores 5 cm in diameter were taken with a soil auger at each position (upper, middle and lower) within the 10 × 50 m plot (Figure S3.1). Independent cores were taken for two sampling depths (0-5 and 5-10 cm). For depth, a composite sample was obtained by mixing the soil from the nine cores. Sealed composite samples were taken to the lab and sieved through a 2 mm mesh to remove gravel and pebbles. C concentration of the fine soil fraction of each composite sample was determined with a mass spectrometer. Dry bulk density was measured with undisturbed soil cores from the same upper, middle, and lower plot positions. Soil samples were sieved and the fine fraction oven-dried at 80°C during three days and weighed. Bulk density was estimated as the ratio between sieved soil mass and the volume of the sample. Soil C stocks for each site were estimated by multiplying C concentrations by mean bulk density of each site and depth.

Statistical analyses

Carbon stocks in relation to forest age

To test if age explained differences in C stocks across forests, four different nonlinear models (hereafter called chronosequence models, Table S3.2) were fitted following previous studies (Sierra *et al.*, 2012; Orihuela-Belmonte *et al.*, 2013; Mora *et al.*, 2015). All

of them assume an asymptotic C accumulation along succession. Old-growth forest sites were assigned 100 years of forest age, since model parameters did not change in relation to the age assigned to old-growth forests (results not shown, see also Mora *et al.*, 2015). The best-fit model for each C pool was selected based on minimization of AICc and confidence intervals for its parameters were derived from fitting the model to one thousand bootstrapped samples. Age needed to reach 50 % of the stock levels at the asymptote was also derived from the fitted models. Model fitting was performed with the `nls` function in R (R Development Core Team, 2011). To ensure that significant fitting of the models was due to an age effect of secondary forests and not to the inclusion of old-growth forests, Spearman correlations between age and stocks were calculated including only secondary forests. Also, *t*-tests were performed to compare secondary and old-growth forests, for those pools not showing a relationship with forest age.

Association across C pools along succession

To assess if and how pools changed along succession in relation to other pools, we tested associations among all possible pairs of pools using Spearman correlations. For highly correlated pools (Spearman $\rho > 0.71$, $P < 0.01$), we fitted linear and power models to provide functions that can be used for C stock estimation. The best-fit model for each association was that show the highest R^2 (since all models had only one independent variable).

To summarize the association between C pools along succession, we constructed a conceptual model of hypothetical causal relations among them (Figure S3.2) and tested it with exploratory path analysis. The model was based on patterns of C allocation in plants and C fluxes among pools (Niklas, 2004; Malhi, 2012). ABC was proposed as the only pool directly influenced by forest age, since it accounts for the interplay between net primary productivity (tree growth) and tree or stem mortality. Other C pools were hypothesized to change in response to ABC rather than to forest age. RC changed as a result of its allometric relation with ABC. LC was functionally linked to ABC due to the increased litterfall from greater foliage and stem mortality as ABC increased. SC was associated to both RC and LC because of increased C inputs to soil from greater stocks of dead plant material above and below the soil surface.

We tested the model with exploratory path analysis through a d-separation test (Shipley, 2000). The null hypothesis of a exploratory path analysis is that the observed associations among the components of a system can be satisfactorily accounted for by the causal multivariate hypothesis represented in a path diagram, so that no additional causal

relations are required (those additional relations are therefore referred as “conditional independence claims”). The test proceeds through testing simultaneously all the conditional independence claims between pairs of variables implied by the hypothesized model. The aim of the test is therefore not to reject the null hypothesis. The test uses the Fisher’s G statistic, which follows a Chi-square distribution with $2k$ degrees of freedom, where k is the minimum number of conditional independence claims to be tested. Further details are found in Shipley (2000). The test was performed using the `ggm` package for R (Marchetti *et al.*, 2012) based on a Spearman correlation matrix, allowing for nonlinear relations between variables. Mean site values for each pool (for 12 sites) were included in the analysis. We recognize sample size is small and therefore the results are taken as indicative of the causal relations among pools (an exploratory analysis), rather than a confirmation of the conceptual model.

Predictive ability of the chronosequence model on observed changes in aboveground biomass carbon stocks of trees

We tested if the chronosequence could predict C stock changes in ABC_T with time by comparing the observed changes in stocks, calculated from repeated measurements in the plots, to the mean expected changes predicted by chronosequence models. Observed changes ($dABC_T$) were calculated by using two previous tree measurements performed in 2004 and 2007 on the same plots and following the previously described approach for stock estimation. Observed changes were defined as the difference in C stocks for two subsequent measurement dates ($dABC_T = ABC_{T+dt} - ABC_T$, where $dt = 3$ years), and were calculated for two periods: 2004 to 2007 and 2007 to 2010. Mean expected changes were derived from chronosequence models with the method proposed by Mora *et al.* (2015). It consists in bootstrapping chronosequence models to estimate the mean and confidence intervals for expected $dABC_T$ along the chronosequence age range.

If chronosequences were good predictors of changes along succession, the statistical model of the relationship between age and observed $dABC_T$ should fall within the confidence intervals for expected $dABC_T$. Also, observed and expected changes should be correlated, so we additionally tested this expectation with Spearman correlations. To derive expected changes for the two periods, two different chronosequence models were fitted using ABC_T data for the initial year of the period in question (2004 and 2007, respectively).

Explanatory power of tree species diversity and functional attributes for aboveground biomass C stocks and stock changes along succession

To assess the effect of tree diversity on ABC_T and $dABC_T$, we first proposed a conceptual model of causal relations among forest age, tree diversity, ABC_T and $dABC_T$ (Figure S3.3), and then tested it using Structural Equation Modeling. In this model, the effect of age on ABC_T was either direct or mediated by tree diversity. The direct effect was attributable to an increase in stem number and size with succession, which could occur even if they all belonged to the same species. We did not include structural variables to measure this effect because we have no independent estimations of both structure and aboveground biomass. The mediated effect of age through tree diversity was assessed with both species and functional diversity (see below), as complementary dimensions of diversity (Hooper *et al.*, 2005; Villéger *et al.*, 2008; Cardinale *et al.*, 2011). In our model, $dABC_T$ was influenced by both initial C stock size (ABC_T) and tree diversity, such that any relationship between age and stock changes was due to the effect of age on both biomass and tree diversity (Figure S3.3).

Test of the conceptual model was done in a two stage process using Structural Equation Modeling. In the first stage, we performed an exploratory analysis to assess which tree diversity variables were relevant in influencing C stocks or changes in aboveground tree biomass, using 2004-2007 data only. After variable selection, we fit the structural equation model (SEM), which served us as our initial variable model. In a second stage, we used 2007-2010 data to perform a confirmatory analysis of the previously selected model, as a form of cross validation.

During the first stage, a range of tree diversity indicators was calculated for both species and functional diversity. Species diversity was quantified as rarefied species richness (S_{raref}), Shannon (H') and Simpson (D) diversity, and Pielou evenness index (J), all calculated with vegan library in R (Oksanen *et al.*, 2011). Functional diversity was assessed with five plant functional traits (Bhaskar *et al.*, 2014a, 2014b): maximum height (H_{max}), wood density (WD), specific leaf area (SLA), leaf nitrogen concentration (N_{leaf}), and leaf C isotopic composition ($\Delta_{13}C$). These traits have been associated to variation in ABC_T or aboveground woody productivity in tropical and subtropical forests (Becknell, 2012; Conti y Díaz, 2013; Finegan *et al.*, 2015). Community weighted means (CWM) and standard deviations (CWsd) were calculated for each trait. Also, four multidimensional functional diversity indices were calculated: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis). These indices allow to represent different properties of the species distribution along a multidimensional trait space (Villéger *et al.*, 2008; Laliberté y Legendre, 2010).

To explore which tree diversity variables were relevant in influencing C stocks or changes in aboveground biomass, we first tested all pairwise relations among them and ABC_T or $dABC_T$ for the 2004-2007 period. While we only sampled 12 plots, we took many samples within each plot. During sampling, each 20×50 m plot was subdivided in five 20×10 m parallel subplots (Figure S3.1). Only data for the secondary forests sites were included in the analysis, so we could assume linear relationships among variables, particularly with forest age (*total* $n = 45$). As samples were non-independent based on the design of the study, we fitted linear mixed effect models using the nlme package in R (Pinheiro *et al.*, 2013), to account for the nested structure of the data (Pinheiro y Bates, 2000). For both species diversity and functional diversity we included in the SEM model the variable that was best associated to ABC_T or $dABC_T$. Variable selection was based on minimization of AICc. We then fit a SEM using a graph theoretic approach (Grace *et al.*, 2012) with mixed effects models to account for the nested structure of the data. Based on variable selection procedures (see Results) our model assessed the direct and indirect effects of H' and CWM on ABC_T and $dABC_T$. We assessed the model for missing paths using a test of d-separation (Shipley, 2009). Our fit SEM then allowed us to explore the direct and indirect effects of the selected diversity variables on both C stocks and stock changes in aboveground tree biomass. Finally, during the second stage of the conceptual model test, we performed a confirmatory analysis of the final model selected in the previous exploratory stage, using 2007-2010 data. The confirmatory test was done using Structural Equation Modelling as described above.

Results

Carbon stocks in relation to forest age

Total ecosystem C stocks ranged from 30.3 to 76.8 Mg C ha⁻¹ (Table S3.1), and were significantly associated to forest age, with 93 % of the variation explained by the chronosequence model (Table S3.2). The association between C stock and age depended on the particular pool considered (Table S3.2, Figure 3.1). As a consequence, the relative contribution of each pool to the total stock changed throughout the chronosequence (Figure S3.4).

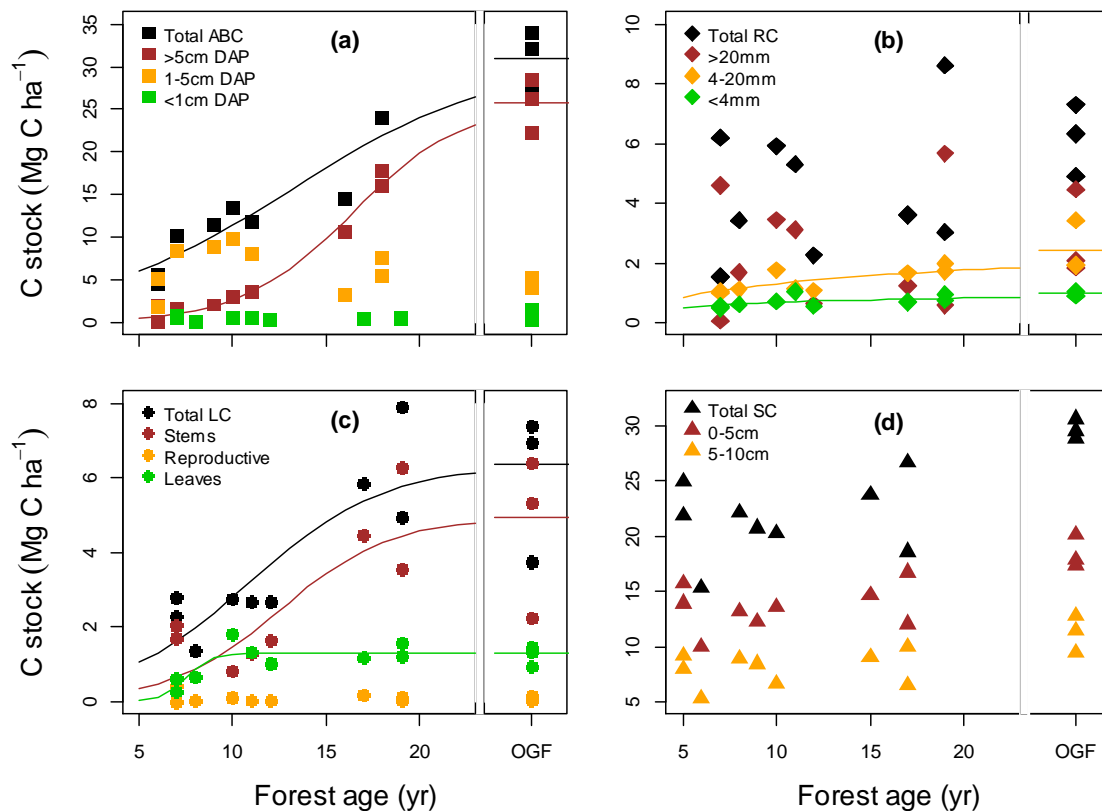


Figure 3.1. Trends of C stocks with forest age in secondary tropical dry forests in the Chamela-Cuixmala region, western Mexico. a) Aboveground living biomass (ABC), b) Roots (RC), c) Surface litter (LC), and d) Soil (SC). Lines represent mean chronosequence trajectories from fitted nonlinear models (see Table S3.2 for model parameters) for those C pools showing a significant relationship with forest age. OGF: Old-growth forest sites.

Total ABC varied between 4.6 Mg C ha⁻¹ in one of the youngest site to 33.9 Mg C ha⁻¹ in an old-growth forest (Table S3.1). Age significantly explained 93 % of the variation in ABC, with an expected age of 12 yr to attain half the asymptotic stock level of 31 Mg C ha⁻¹ (Table S3.2). Within the ABC pool, only C in trees > 5 cm DBH showed a significant association with age (Table S3.2, Figure 3.1). Neither ABC in herbs or trees 1-5 cm DBH differed between the group of nine secondary forests and the group of three old-growth forests ($t = 0.91$ and -1.18 for herbs and trees, respectively; $df = 10$ and $P > 0.1$, in both cases).

Total RC ranged from 1.5 to 8.6 Mg C ha⁻¹ (Table S3.1), with no significant relationship to age (Table S3.2, Figure 3.1) and no difference between secondary and old-growth forests ($t = 1.26$, $df = 10$, $P > 0.1$). C stocks in both small and medium-sized roots were significantly related to age (Table S3.2, Figure 3.1), with 5 and 10.8 yr to reach half the

expected asymptotic stocks, respectively. Large root C showed no significant trend with age nor was different between secondary and old-growth forests ($t = 0.37$, $df = 10$, $P > 0.1$).

Total LC varied between 1.4 and 7.9 Mg C ha⁻¹ (Table S3.1), and age significantly explained 69 % of its variation (Table S3.2). As many as 10.8 yr would be needed to reach half the asymptotic LC value. Both the leaves and stems fractions showed a significant relationship with age (Table S3.2, Figure 3.1). The reproductive fraction showed no trend and was not different between secondary and old-growth forests ($t = -0.09$, $df = 10$, $P > 0.1$).

Soil C ranged from 15.3 to 30.6 Mg ha⁻¹ (Table S3.1). No consistent pattern of relationship was found between age and soil C. Age explained significantly Soil C for all depth categories, but Spearman correlations showed no association between forest age and Soil C for secondary forests only (Table S3.2). Therefore, the apparent association seems to arise from including old-growth forest sites in nonlinear models. Mean soil C stocks in old-growth forests were significantly higher than those in secondary forest (means' difference = 8.1 Mg C ha⁻¹, $t = 3.96$, $df = 10$, $P < 0.01$). The same pattern was found by soil depth with age ($t = 3.81$, $df = 10$, $P < 0.01$ at 0-5 cm; $t = 3.10$, $df = 10$, $P < 0.05$ at 5-10 cm).

Association across C pools along succession

Significant correlations were found between several pairs of C pools (Table S3.3). Particularly relevant for stock estimation were those associations found between total ABC and both small and medium sized roots (< 20 mm) and total LC. Added together, small and medium-sized roots ($RC_{<20}$) showed a linear relationship with ABC, which explained 75 % of the variation in this pool (Figure 3.2a). From this relationship, a decreasing root < 20 mm:shoot C ratio as ABC increases can be derived (Figure S3.5). LC showed a power relationship with ABC, explaining 51 % of its variation (Figure 3.2b). A significant association was also found between SC and ABC in trees < 5.0 cm DBH (Figure 3.2c), which explained 55 % of the variation in soil C.

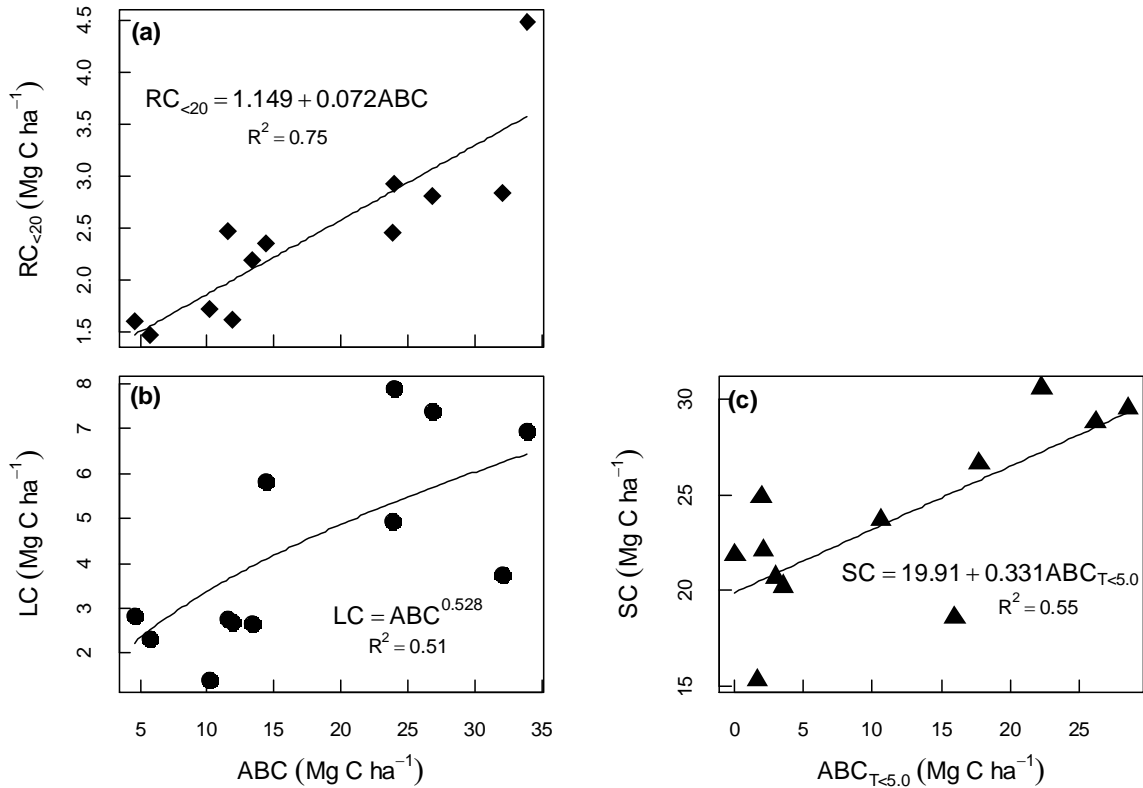


Figure 3.2. Relationships between biomass C pools across a chronosequence of secondary tropical dry forests in the Chamela-Cuixmala region, western Mexico. C in roots < 20 mm diameter ($RC_{<20}$) (a) and C in surface litter (LC) (b) are shown as a function of the total aboveground biomass C stock (ABC). Soil C (SC) is shown as a function of C in the aboveground biomass of stems > 5.0 cm DBH ($ABC_{T<5.0}$).

Our model depicting causal relationships between forest age and ABC, RC and SC pools was supported by the confirmatory path analysis ($C = 8.61$, $df = 10$, $P = 0.57$, Figure 3.3). As expected, ABC showed a high correlation with age. LC was associated to ABC. $RC_{<20}$ was included in the model rather than total RC, since the latter showed no relation with ABC (Table S3.3). Its inclusion, nevertheless, did not affect model support ($C = 9.18$, $df = 10$, $P = 0.52$). Contrary to our hypothesis, there was no evidence of association between soil C and surface litter or roots < 20 mm C (Figure 3.3, Table S3.3).

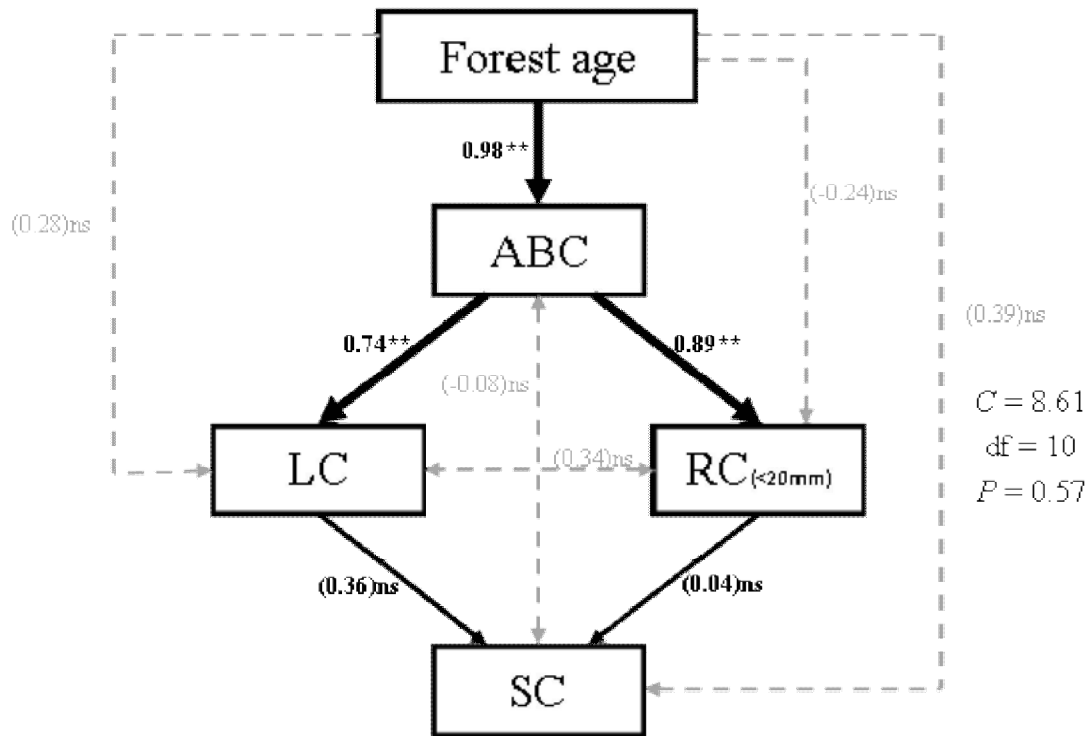


Figure 3.3. Path analysis testing the causal relationships among forest age and C pools in secondary and old-growth tropical dry forests in the Chamela-Cuixmala region, western Mexico. Black arrows are hypothesized causal relationships. Grey dashed lines represent conditional independence claims used to test the whole model. The test of the model is given on the right. Values on arrows are Spearman correlations, with partial correlations in parentheses. ^{**} $P < 0.01$, ^{*} $P < 0.05$, (^{*}) $P < 0.1$, ns: non-significant. ABC: Carbon in aboveground living biomass, LC: surface litter C, $RC_{<20mm}$: C in roots < 20 mm diameter, SC: C in the top 10 cm of soil.

Predictive ability of the chronosequence model on observed changes in aboveground biomass C of trees

Observed changes in tree aboveground biomass C varied between -1.33 and $4.46 \text{ Mg C ha}^{-1} \text{ 3yr}^{-1}$ for the 2004-2007 period, and between 0.42 and $7.14 \text{ Mg C ha}^{-1} \text{ 3yr}^{-1}$ for the 2007-2010 period (Figure 3.4, Table S3.4). Mean observed $dABC_T$ differed significantly between the two periods ($1.38 \text{ Mg C ha}^{-1} \text{ 3yr}^{-1}$ for 2004-2007; $3.09 \text{ Mg C ha}^{-1} \text{ 3yr}^{-1}$ for 2007-2010; paired t test: $t = -2.99$, $df = 11$, $P < 0.05$). Observed $dABC_T$ was not significantly different between secondary and old-growth forests in the 2004-2007 period ($1.64 \text{ Mg C ha}^{-1} \text{ 3yr}^{-1}$ for secondary forests, $0.61 \text{ Mg C ha}^{-1} \text{ 3yr}^{-1}$ for old-growth forests; $t = 0.73$, $df = 10$, $P > 0.1$), nor in the second period ($3.54 \text{ Mg C ha}^{-1} \text{ 3yr}^{-1}$ for secondary forests, $1.76 \text{ Mg C ha}^{-1} \text{ 3yr}^{-1}$ for old-growth forests; $t = 1.46$, $df = 10$, $P > 0.1$).

No significant relationship was found between observed $dABC_T$ and forest age for the 2004-2007 period. A significant, but very loose relationship was found for the 2007-

2010 period (Figure 3.4, Table S3.5). The chronosequence showed a very low ability to predict observed changes in ABC_T . Models fitted to observed $dABC_T$ did not fall within the confidence intervals for expected $dABC_T$ (Figure 3.4), nor were observed and expected $dABC_T$ values correlated for any of the two periods ($r = -0.36$, $P = 0.35$ for 2004-2007 period; $r = 0.07$, $P = 0.86$ for 2007-2010 period).

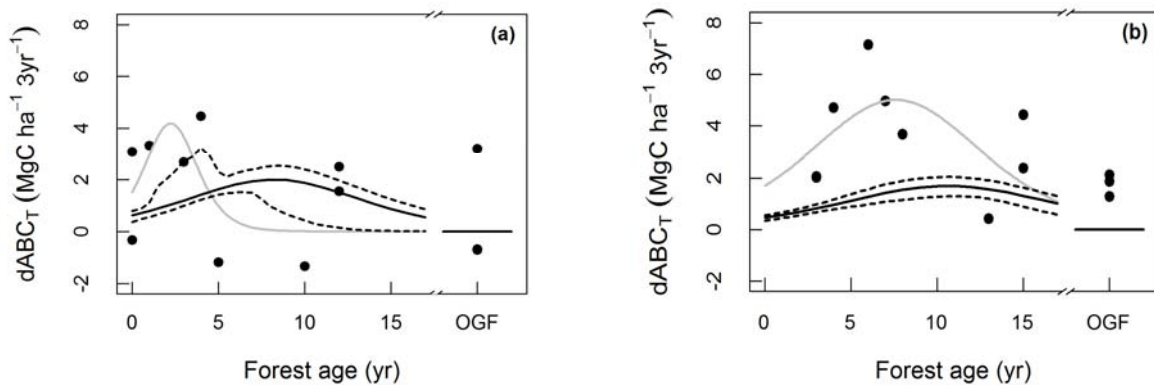


Figure 3.4. Observed C accumulation rates in tree aboveground biomass ($dABC_T$) in relation to forest age in secondary tropical dry forests in the Chamela-Cuixmala region, western Mexico. Observed changes were evaluated for two periods: from 2004 to 2007 (a), and from 2007 to 2010 (b). Grey continuous lines represent the model fitted to observed changes. Black continuous lines represent mean expected changes from chronosequence models fitted to ABC_T ; dotted lines indicate the 95 % confidence intervals. OGF: old-growth forest sites.

Species diversity, functional attributes and carbon stocks

Several indices and variables of species and functional diversity were significantly related to either ABC_T stocks or observed $dABC_T$ (Table 3.1). The Shannon and inverse Simpson diversity indices (H' and $invD$, respectively) showed a positive relation with initial ABC_T , while Pielou evenness index (J) showed a negative relation. The observed $dABC_T$ was not associated to any of the species diversity indexes. H' was included in the SEM as an indicator of species diversity since it was best associated to ABC_T as indicated by the AICc values (Table 3.1).

The community weighted mean of maximum height (H_{max} CWM), the standard deviation of the isotopic C content in leaves ($d_{13}C$), as well as the functional richness and divergence indices (F_{rich} and F_{div}) explained the variation in initial ABC_T (Table 3.1). Among the variables tested, only H_{max} CWM showed a significant relationship with stock $dABC_T$. Since H_{max} CWM showed the strongest relationship with initial C stocks and stock changes (Table 3.1), it was included as an indicator of functional diversity in the SEM.

Table 3.1. Species and functional diversity indices with a statistically significant association ($P < 0.05$) with tree aboveground biomass C stock (ABC_T) or its change ($dABC_T$) in secondary tropical dry forests in the Chamela-Cuixmala region, western Mexico. Relationships were evaluated with mixed-effects models. Predictors acronyms are: H' (Shannon index), $invD$ (Inverse Simpson index), J (Pielou evenness index), H_{max} (maximum tree height), isotopic carbon ($d13C$), Frich (functional richness index), $FDiv$ (functional divergence). CWM: community weighted mean, CWsd: community weighted standard deviation.

Variable type	Response variable	Predictor variable	Coefficient	<i>df</i>	<i>t</i>	<i>P</i>	AICc
Species diversity	ABC_T	H'	1.58	24	4.3	< 0.01	108.5
		$invD$	0.182	24	2.6	< 0.05	117.7
		J	-6.672	24	-2.3	< 0.05	110.3
	$dABC_T$	<i>none</i>					
Functional diversity	ABC_T	H_{max} CWM	0.769	21	4.22	< 0.01	98.9
		Frich	0.263	21	6.21	< 0.01	102.8
		Fdiv	3.96	21	2.18	< 0.05	104.1
		$d13C$ CWsd	1.955	21	2.25	< 0.05	105.7
		H_{max} CWsd	0.811	21	2.16	< 0.05	108.6
	$dABC_T$	H_{max} CWM	0.14	21	2.5	< 0.05	31.84

Our exploratory model relating forest age, species diversity (H'), functional diversity (H_{max} CWM), ABC_T and $dABC_T$ for the 2004-2007 period was supported ($C = 5.15$, $df = 4$, $P = 0.27$; Figure 3.5a). ABC_T was directly predicted by forest age and indirectly through the effect of forest age on H_{max} CWM. The overall relationship was positive since effect sizes in both paths were positive. There was no significant effect of species diversity (H') on ABC_T stocks. The total standardized effect size of forest age on ABC_T given by the statistically significant paths was 0.74. From the total effect of forest age on ABC_T , 22 % was mediated by H_{max} CWM. Both H_{max} CWM and ABC_T were related to $dABC_T$ (Figure 3.5a). $dABC_T$ decreased as ABC_T increased, whereas the effect of H_{max} CWM was positive. As a result, the total effect size of forest age on $dABC_T$ was low and negative: the effect of forest age mediated by ABC_T was -0.29, and the mediated effect of H_{max} CWM was 0.22, with a total effect size of -0.07. That is, forest age did not predict the observed changes in tree biomass C due to its counteracting effects through C stock size and functional diversity. Species diversity (H') had no significant effect on $dABC_T$.

The confirmatory model was also supported by the test of d-separation ($C = 7.73$, $df = 4$, $P = 0.10$; Figure 3.5b). However, in this model the ability to explain observed C stock changes through time differed from the exploratory model: $dABC_T$ was not related to H_{max} CWM or ABC_T (Figure 3.5b). Also, there was a significant relationship between species

diversity (H') and functional diversity (H_{\max} CWM) not previously found in the exploratory model, although the direct effects of H' on ABC_T and $dABC_T$ remained non-significant.

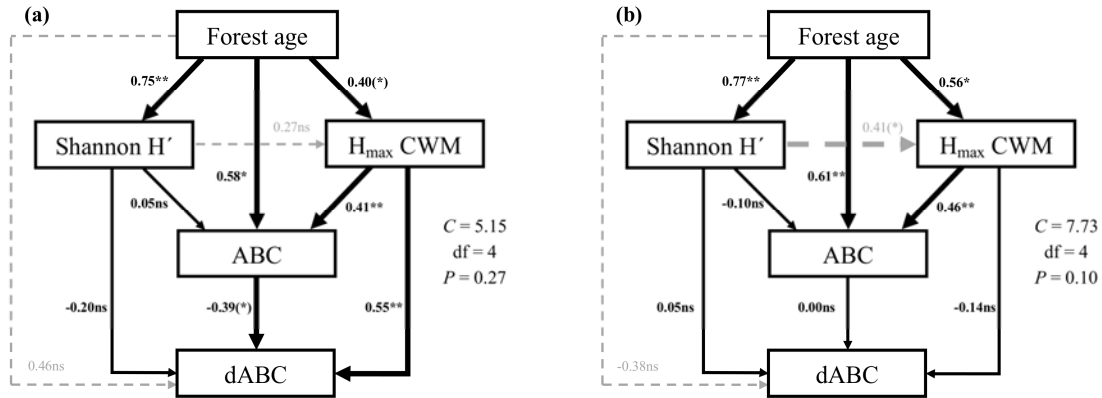


Figure 3.5. Exploratory (a) and confirmatory (b) structural equation models testing the causal relationships among forest age, tree diversity and aboveground carbon stocks (ABC) and their change through time (dABC) in secondary tropical dry forest in the Chamela-Cuixmala region, western Mexico. The exploratory analysis (a) was performed for 2004-2007 period data, while the confirmatory analysis (b) was done on 2007-2010 data. Shannon diversity index (H') was included as an indicator of species diversity and the community weighted mean of maximum tree height (H_{\max} CWM) as an indicator of functional diversity. Black arrows are hypothesized causal relationships. Grey dashed lines represent conditional independence claims used to test the whole model. The test for each model is given on the right. Values on arrows are standardized effect sizes. ** $P < 0.01$, * $P < 0.05$, (*) $P < 0.1$, ns: non-significant.

Discussion

Forest age and maximum tree height as drivers of C stocks

Carbon accumulated in secondary forests as they aged, driven by increases in aboveground tree biomass, surface litter, and small to medium sized roots (< 20 mm). The positive relationship shown by these C pools with forest age is consistent with results from the few previous studies in other TDFs (Vargas *et al.*, 2008; Kissing y Powers, 2010; Becknell *et al.*, 2012). The recovery of these three C pools seems to be the result of an integrated increase in plant biomass, as the exploratory analysis of our hypothesized conceptual model indicates, rather than independent responses of each C pool to increased age. Allometric

theory predicts gradually decreasing increments in both leaf and root mass as shoot mass increases (Niklas, 2004). The relationships found between aboveground biomass C and both surface litter C and root (< 20 mm) C support this general expectation (Niklas, 2004; Mokany *et al.*, 2006). Residence time of fine litter is about 1-2 years (Martínez-Yrizar, 1995; Anaya *et al.*, 2012), which suggests that the sampled litter came mostly from the immediately previous growing season. Alternatively, the reduced root (< 20 mm):shoot C ratio could also result from changes in biomass allocation in response to a reduction in water stress, as soil water availability increases during secondary succession (Lebrija-Trejos *et al.*, 2011; Pineda-García *et al.*, 2013), causing shifts in root morphology and root biomass allocation (Markesteyn y Poorter, 2009; Roa-Fuentes *et al.*, 2012; Paz *et al.*, 2015). The suggested integrated response of plant biomass results in the recovery of ca. 75 % of the biomass C stocks after 18 yr of secondary succession, driving the recovery of the total ecosystem C stock of the Chamela TDF.

Functional properties of the tree community, particularly maximum tree height, also influenced C stocks in these secondary forests. The positive relationship between the CWM of maximum tree height and aboveground tree biomass C indicates that as the tree community is composed of species able to attain larger sizes, the whole community stores more C. Similar results were documented in successional subtropical forests (Conti y Díaz, 2013) and matches the observed pattern of higher C stocks in stands with greater abundance of large trees (Balvanera *et al.*, 2005; Slik *et al.*, 2013), and higher accumulation rates in bigger trees (Stephenson *et al.*, 2014; Fauset *et al.*, 2015). Our analytical approach also shows that this association arises not only from a correlation of both biomass and functional traits with forest age (Becknell *et al.*, 2012; Lohbeck *et al.*, 2013), but also from an increase in the average value of this trait as the forest ages. Therefore, aboveground tree biomass C increases not only because of the increase in tree density and growth as succession proceeds (*i.e.* a structural effect), but also because it is driven by changes in the species composition of the tree community and their effect on traits like maximum tree height (Barrufol *et al.*, 2013; Conti y Díaz, 2013).

Other relevant C pools, namely large roots and soil, showed no discernible change with succession. The lack of a trend in large-root C with forest age was unexpected given previous evidence from other studies in the dry tropics (Jaramillo *et al.*, 2003b; Costa *et al.*, 2014) and the allometric relation between aboveground and belowground biomass (Mokany *et al.*, 2006). Large variation within and across sites in the presence of root remnants from tree stumps suggests that prior species composition, slow large-root decomposition rates and previous land use may determine the magnitude of this pool. The type, frequency and length of previous land use has been proposed to affect the magnitude

of other C pools, sometimes blurring the effect of forest age (Eaton y Lawrence, 2006; Kissing y Powers, 2010; Orihuela-Belmonte *et al.*, 2013). In contrast, the lack of association between soil C and forest age and the lower soil C stock in secondary forests when compared to old-growth forests are in agreement with previous studies throughout the tropics (Hughes *et al.*, 1999; Don *et al.*, 2011; Marin-Spiotta y Sharma, 2013). Changes in soil C depend more strongly on factors not directly related to forest age or biomass recovery. Since estimation of soil C stocks depends on both C concentration and soil bulk density (Murty *et al.*, 2002; Don *et al.*, 2011), it is likely that the large variation in soil bulk density (0.90 to 1.54 g cm⁻³; see Cotler *et al.*, 2002), unrelated to forest age in our study, resulted in a lack of a relationship between forest age and soil C stocks. It is also possible that increased soil C inputs from roots and surface litter to the soil during succession result in higher microbial activity and soil respiration (García-Oliva *et al.*, 1994; García-Oliva y Jaramillo, 2011) and thus a lack of apparent change in total soil C.

Water availability modifies the influence of forest age, biomass and tree diversity on C stock changes

Observed C stock changes in aboveground tree biomass were not driven by forest age. C stock changes were found to be partially driven by aboveground biomass and maximum tree height in our exploratory SEM fitted with the 2004-2007 data, but such effects did not remain significant in the confirmatory model fitted for the 2007-2010 period. We hypothesize that differences in annual and seasonal distribution of rainfall could cause the differential expression of C accumulation drivers between periods, since the main environmental driver of ecological processes in TDF is water availability (Borchert, 1994; Segura *et al.*, 2003; Anaya *et al.*, 2012). The 2004-2007 period included two very dry years (40 % below average), while 2007-2010 included two consecutive years of higher than average rainfall (22 % above average) (Figure S3.6). The low or even negative ABC accumulation rates observed during the first period could be associated to increased drought induced tree mortality (F. Mora *et al.*, unpublished), while higher C accumulation rates during the second period could be explained by greater tree growth (F. Mora *et al.*, unpublished) as water availability increased (Ciais *et al.*, 2005; Phillips *et al.*, 2009). Previous work in the Chamela TDF has suggested that functional differences among species are greater in drier than wetter years (Rentería y Jaramillo, 2011). Also, the role of diversity on ecosystem functioning varies through water availability gradients (Steudel *et al.*, 2012; Grossiord *et al.*, 2014). It seems that when conditions were more stressful (2004-2007), the functional differences among species were expressed and may have reflected in species-specific growth and mortality rates (Poorter *et al.*, 2008). When conditions were less

restrictive (i.e. more water available during 2007-2010), all species performed relatively uniformly, as suggested by the exploitative strategy (Pineda-García *et al.*, 2011), resulting in higher C accumulation rates

Implications for C stocks and C accumulation estimation

The statistical relations among C stocks found in our study could be used to estimate root < 20 mm and surface litter C stocks in secondary tropical dry forests. This may be particularly useful given the now more widely available aboveground biomass C values at both local and regional scales (Goetz *et al.*, 2009; Asner *et al.*, 2010). Such approach has been recently used to estimate total plant biomass C stocks and emissions from deforestation in tropical regions (Saatchi *et al.*, 2011; Harris *et al.*, 2012). However, the lack of association between aboveground biomass C and large root (> 20 mm) C also imply that the equations and root:shoot ratios widely used to estimate total belowground biomass from aboveground biomass (IPCC, 2006; Mokany *et al.*, 2006) provide biased estimates of root C in secondary forests (Kenzo *et al.*, 2010). Such equations may not be applicable in situations where root remnants after deforestation are common, like in most of our study sites.

Chronosequence models proved to be poor predictors of short-term (3-year period) C stock changes through succession. Similar results have been reported for structural and diversity attributes of the tree and seedling communities along this chronosequence (Maza-Villalobos *et al.*, 2011; Mora *et al.*, 2015) and for biomass changes through time in recently abandoned pastures in Amazonia (Feldpausch *et al.*, 2007). This has important implications concerning the role of tropical secondary forests in the global C cycle. Several studies have used chronosequences to infer rates of biomass or C accumulation during succession (see for example Vargas *et al.*, 2008; Yang *et al.*, 2011; Orihuela-Belmonte *et al.*, 2013). Also, IPCC guidelines provide biomass accumulation values derived from chronosequence studies (IPCC, 2006) and a recent meta-analysis on this topic was mostly based on studies following such an approach (Bonner *et al.*, 2013). All provide estimates of C stock change well above the observed values in our study.

Our results suggest that indeed chronosequences may overestimate C accumulation rates along succession. Based on IPCC guidelines, a mean stock change of 5.76 Mg C ha⁻¹ 3yr⁻¹ would be expected for secondary TDFs occurring in regions below 1000 mm of annual rainfall and less than 20 yr old. Estimates for forests on the same age range derived from Bonner *et al.* (2013) yield a mean value of 10.8 Mg C ha⁻¹ 3yr⁻¹, although this meta-analysis did not include TDFs *sensu stricto*. Our observed accumulation rates, averaged over the two periods and across the nine secondary forest sites, was 2.59 Mg C ha⁻¹ 3yr⁻¹, with only one

site-period combination above the estimate from IPCC guidelines and none above Bonner *et al.* (2013) estimate. Our results therefore suggest that the role of secondary tropical forests in the global C cycle could be overestimated, as recent studies has also suggested (Achard *et al.*, 2014) should be re-assessed. Further measurements of biomass C accumulation rates derived from repeated measurements in secondary forests are needed to provide more accurate estimates.

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Figure S3.1. Sampling design used for the estimation of carbon stocks in four different ecosystem pools in nine secondary and three old growth tropical dry forests in the Chamela-Cuixmala region, western Mexico. At each site a 20 x 50 m plot was established. For the estimation of aboveground biomass carbon in trees (ABC_T), all live woody stems inside the plot were measured in a nested array: stems > 1.0 cm DBH were measured in half the plot (light green area on the left figure), and stems > 2.5 cm DBH on the other half (dark green area on the left figure). Additionally, herbaceous biomass carbon (ABC_H) was estimated by harvesting all plants < 1 cm DBH in three 2.0 x 0.5 m plots (brown rectangles just outside the 20 x 50m plot). Surface litter carbon (LC) was estimated from forest floor litter samples taken in nine 30 x 30 cm plots (orange quadrants) located in the upper, middle and lower locations of the 10x50m plot used for measuring trees > 1.0 cm DBH, with three microplots located at random in each portion. Carbon in roots was estimated from direct sampling of roots inside the three 2.0 x 0.5 m plots (brown rectangles) used for ABC_H estimation, down to 40cm depth. Soil carbon (SC) and soil bulk density (SBD) were estimated from three and one soil cores (dots on the right figure), taken at each of the three locations (upper, middle and lower) of the 10x50m plot, respectively. ABC_T values used in confirmatory path analysis were obtained from subdividing the 20 x 50m plot into five parallel 20 x 10 m plots in each site (left figure) and including only data from stems > 2.5 cm DBH.

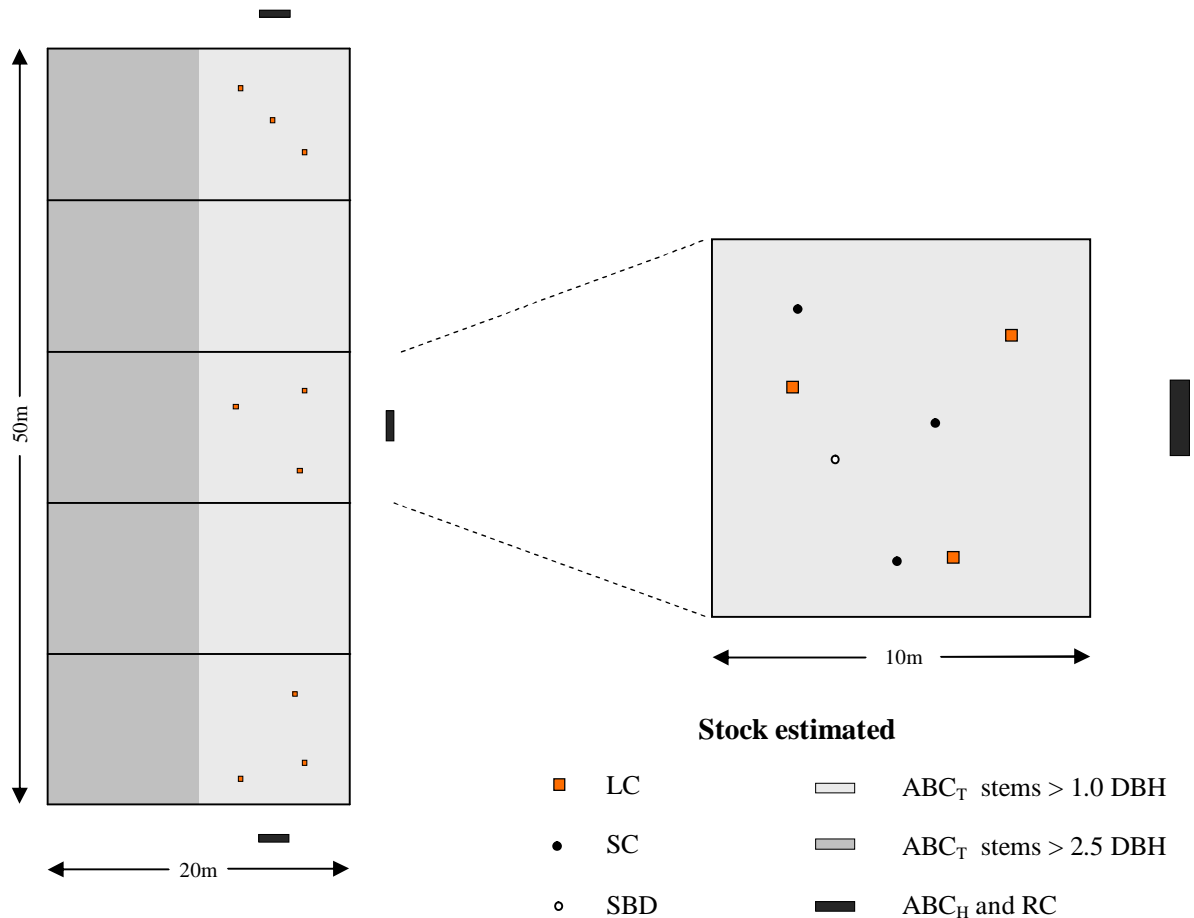


Figure S3.2. Conceptual model showing the hypothesized causal relations between carbon pools along tropical dry forest secondary succession. Black continuous lines represent the hypothesized causal relations, while grey dashed lines (known as conditional independence claims) represent those associations not assumed to be causal and therefore not expected to be significant after accounting for causal relations. Forest age: time elapsed after land abandonment, ABC: aboveground biomass carbon, LC: surface litter carbon, RC: root carbon, SC: soil carbon.

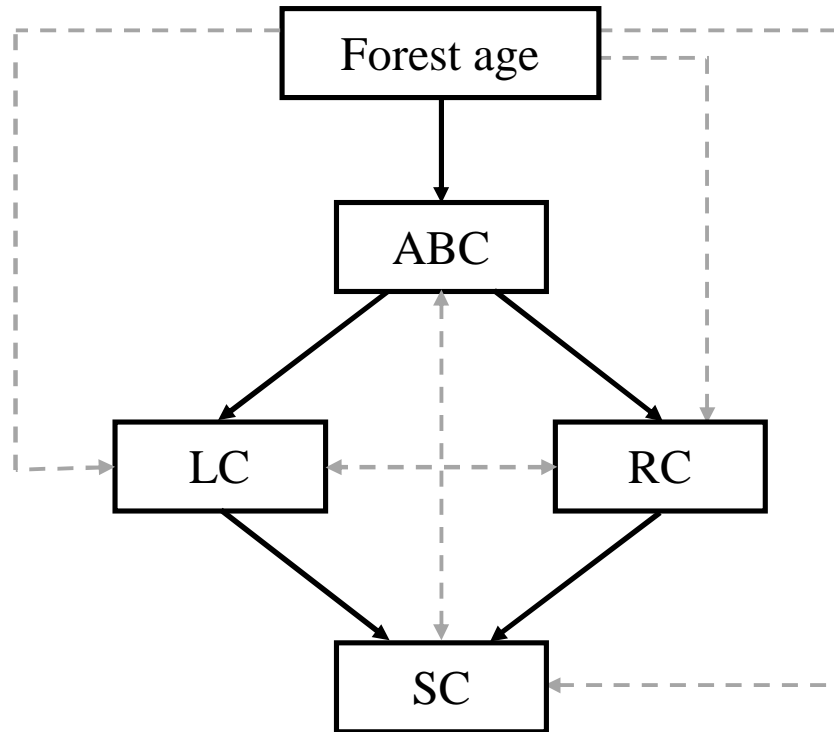


Figure S3.3. Conceptual model showing the hypothesized causal effects of forest age (Age), tree species diversity and tree functional diversity on carbon stocks in aboveground biomass of trees (ABC_T) and their observed change through time ($dABC_T$). Black continuous lines represent the hypothesized causal relations, while grey dashed lines (known as conditional independence claims) represent those associations not assumed to be causal and therefore not expected to be significant after accounting for causal relations.

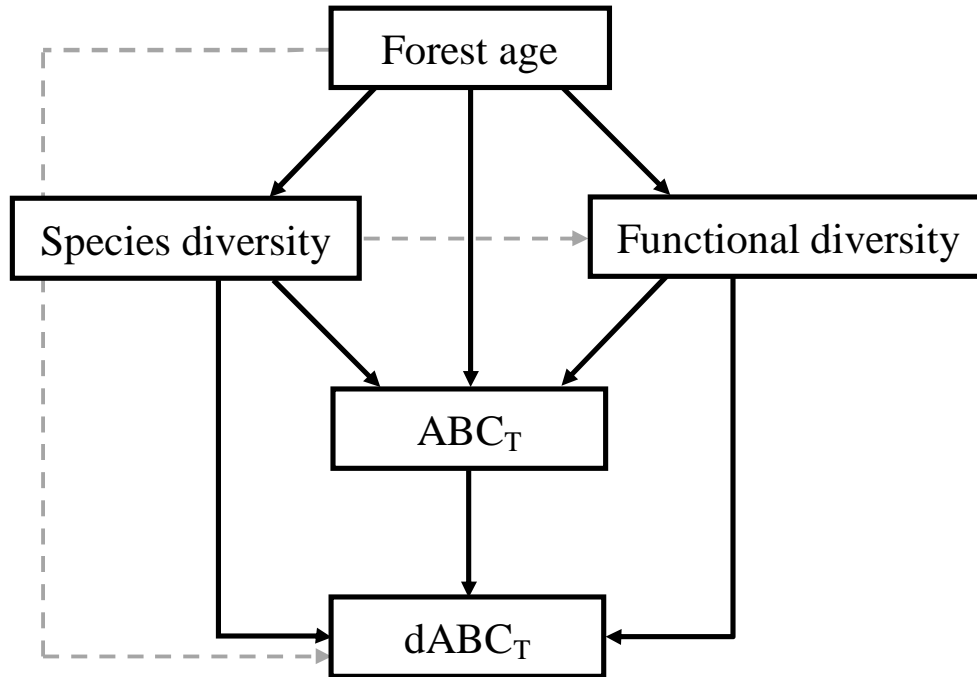


Figure S3.4. Relative contribution of four carbon pools to the total ecosystem stock in nine secondary and three old growth tropical dry forests in the Chamela region, western Mexico. Sites are displayed in ascending order of forest age (years indicated in parenthesis). ABC: aboveground biomass carbon, LC: surface litter carbon, RC: root carbon, SC: soil carbon. OG: old growth forests.

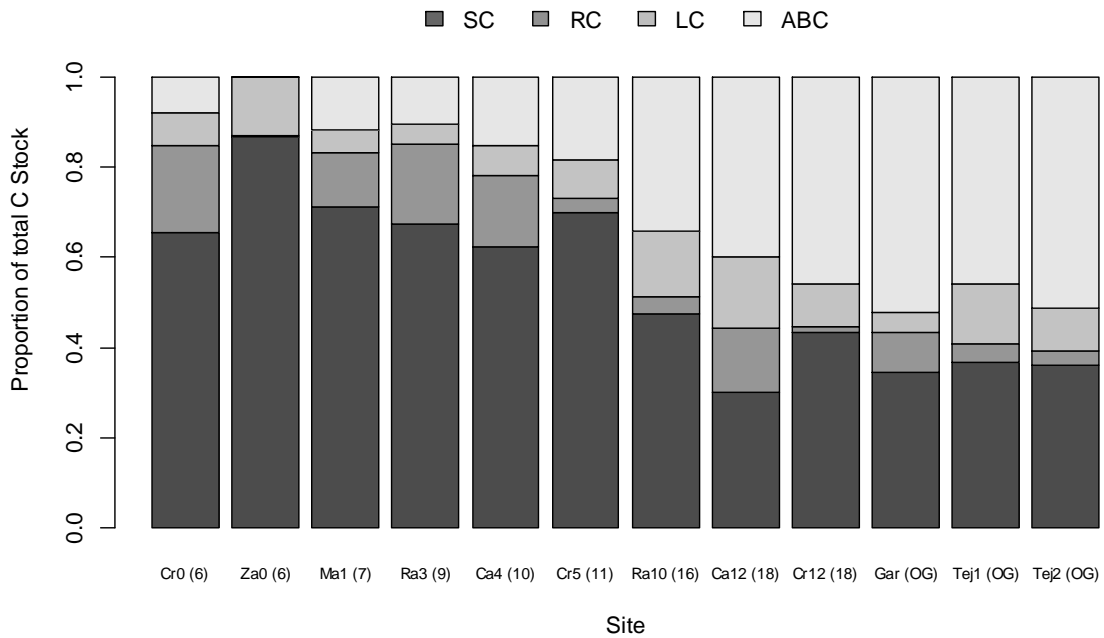


Figure S3.5. Root:shoot C ratio in relation to C in aboveground biomass across in nine secondary and three old growth tropical dry forests in the Chamela region, western Mexico.

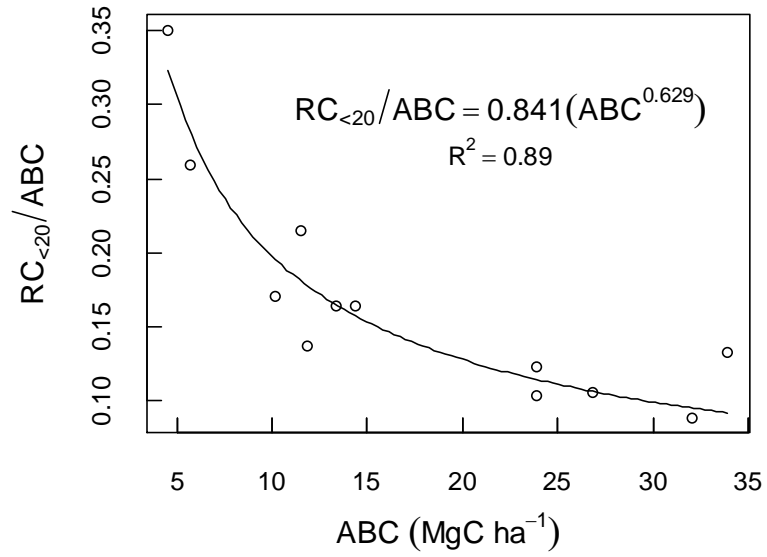


Figure S3.6. Annual precipitation between 1977 and 2012 in the Chamela-Cuixmala region. Red lines indicate different quantiles. Data provided by the "Watershed Project", UNAM.

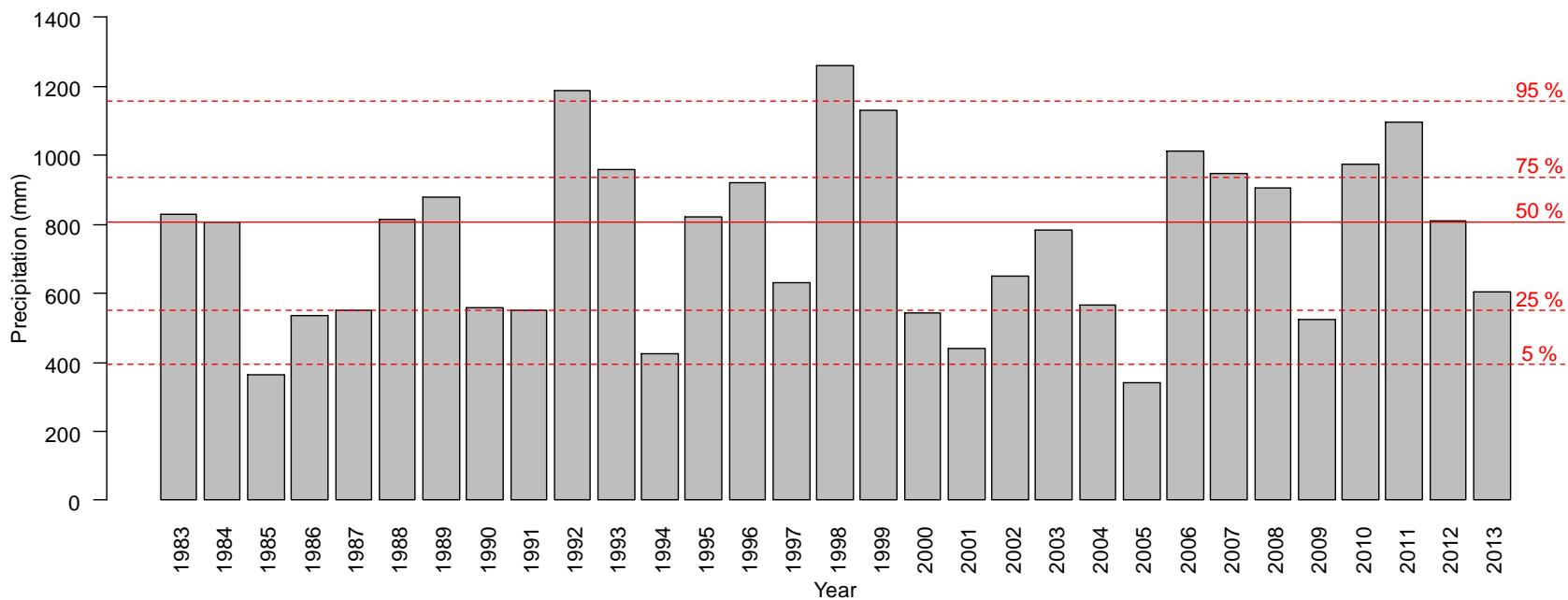


Table S3.1. Ecosystem carbon stocks in nine secondary and three old growth tropical dry forests in the Chamela-Cuixmala region, western Mexico. Sampling dates are indicated in parenthesis. All the values are in Mg ha⁻¹.

Site acronym	Cr0	Za0	Ma1	Ra3	Ca4	Cr5	Ra10	Ca12	Cr12	Gar	Tej1	Tej2
Forest age in 2010 (years)	6	6	7	9	10	11	16	18	18	OGF	OGF	OGF
Aboveground biomass												
Herbs (2011)	0.76	0.55	0.11	0.59	0.64	0.33	0.50	0.39	0.62	1.49	0.41	0.23
Trees 1-5 cm DBH (2010)	1.87	5.11	8.37	8.83	9.74	8.00	3.27	7.56	5.53	4.41	4.14	5.20
Trees > 5 cm DBH (2010)	1.94	0.03	1.67	2.08	2.98	3.55	10.59	15.96	17.72	26.17	22.27	28.51
<i>Total Aboveground biomass</i>	<i>4.57</i>	<i>5.69</i>	<i>10.14</i>	<i>11.5</i>	<i>13.36</i>	<i>11.88</i>	<i>14.36</i>	<i>23.92</i>	<i>23.87</i>	<i>32.06</i>	<i>26.81</i>	<i>33.94</i>
Roots (2011)												
< 4mm diameter	0.57	0.48	0.60	0.71	1.04	0.56	0.69	0.96	0.75	0.91	0.90	1.06
4-20mm diameter	1.04	1.00	1.13	1.76	1.16	1.07	1.67	1.97	1.71	1.92	1.91	3.43
> 20mm diameter	4.59	0.06	1.69	3.45	3.11	0.63	1.24	5.67	0.58	4.46	2.09	1.84
<i>Total Root</i>	<i>6.19</i>	<i>1.53</i>	<i>3.42</i>	<i>5.92</i>	<i>5.31</i>	<i>2.26</i>	<i>3.60</i>	<i>8.60</i>	<i>3.04</i>	<i>7.30</i>	<i>4.91</i>	<i>6.33</i>
Surface litter (2011)												
Leaves	0.65	0.26	0.69	1.80	1.34	1.02	1.17	1.57	1.23	1.35	0.96	1.47
Stems/petioles	1.71	2.05	0.69	0.84	1.29	1.66	4.46	6.27	3.57	2.26	6.39	5.33
Reproductive	0.45	0.00	0.02	0.11	0.04	0.03	0.20	0.05	0.13	0.14	0.04	0.15
<i>Total Surface litter</i>	<i>2.81</i>	<i>2.31</i>	<i>1.40</i>	<i>2.75</i>	<i>2.67</i>	<i>2.70</i>	<i>5.83</i>	<i>7.90</i>	<i>4.93</i>	<i>3.74</i>	<i>7.39</i>	<i>6.94</i>
Soil (2009)												
0-5 cm depth	15.70	13.90	9.98	13.16	12.27	13.57	14.67	12.07	16.70	17.40	17.83	20.09
5-10 cm depth	9.19	7.96	5.34	8.94	8.44	6.65	9.04	6.51	9.97	11.44	12.77	9.45
<i>Total Soil 0-10 cm depth</i>	<i>24.89</i>	<i>21.86</i>	<i>15.32</i>	<i>22.10</i>	<i>20.72</i>	<i>20.22</i>	<i>23.71</i>	<i>18.58</i>	<i>26.67</i>	<i>28.83</i>	<i>30.60</i>	<i>29.54</i>
Total Ecosystem	38.47	31.39	30.28	42.27	42.06	37.07	47.50	59.00	58.50	71.93	69.71	76.75

Table S3.2. The effect of forest age on C stocks along a chronosequence of nine secondary tropical dry forest and three old-growth forest sites in the Chamela-Cuixmala region, western Mexico. The effect of forest age was tested with four different nonlinear models: Michaelis-Menten (Mic-men; $Stock = at/(b + t)$), asymptotic ($Stock = a + (b - a)e^{-e^{ct}}$), Gompertz ($Stock = ae^{-bc^t}$), and logistic ($Stock = (a/(1 + e^{(b-t)/c}))$). Both secondary and old-growth forests were included during model fitting and model selection was based on minimization of AICc. R²: coefficient of determination. Spearman correlations tested the association between each stock and forest age for secondary forests only. ** P < 0.01, *P < 0.05, (*) P < 0.1, ns: non-significant. NA: model fitting was not attainable.

Pool	Model	a	b	c	R ²	Spearman ρ
Aboveground biomass						
Herbs (< 1 cm DBH)	Mic-men	0.69**	3.95ns		0.05	-0.20ns
Trees 1-5 cm DBH	NA					0.09ns
Trees > 5 cm DBH	Logistic	25.71**	16.4**	2.97**	0.98	0.97**
<i>Total Aboveground</i>	Logistic	31**	12.05**	5.62**	0.93	0.98**
Roots						
< 4 mm diameter	Mic-men	1.02**	4.95**		0.52	0.61(*)
4-20 mm diameter	Mic-men	2.7**	10.75**		0.61	0.75*
> 20 mm diameter	Mic-men	2.81**	2.14ns		0.02	0.02ns
<i>Total Root</i>	Mic-men	6.47**	5.09ns		0.18	0.13ns
Surface litter						
Leaves	Logistic	1.32**	7.58**	0.67**	0.66	0.63(*)
Stems	Logistic	4.94**	12.54**	2.95**	0.63	0.56(*)
Reproductive	Mic-men	0.07**	-4.34ns		0.05	0.27ns
<i>Total Surface litter</i>	Logistic	6.35**	10.83**	3.62**	0.69	0.69*
Soil						
0-5 cm depth	Mic-men	17.93**	2.56*		0.48	0.04ns
5-10 cm depth	Mic-men	10.92**	2.91*		0.38	0.09ns
<i>Total Soil (0-10 cm)</i>	Mic-men	28.86**	2.69*		0.46	0.03ns
Total Ecosystem	Mic-men	79.73**	8.82**		0.93	0.80**

Table S3.3. Spearman correlations between carbon pools across nine tropical dry secondary and three old-growth forests in the Chamela-Cuixmala region, western Mexico. ABC: Aboveground biomass carbon, RC: root carbon, LC: surface litter carbon, SC: soil carbon. Significance levels are: ** $P < 0.01$, * $P < 0.05$, (*) $P < 0.1$.

	ABC _H	ABC _{T<5.0}	ABC _{T>5.0}	ABC _{Total}	RC _{<4.0}	RC _{4.0-20}	RC _{<20}	RC _{>20}	RC _{Total}	LC _{leaves}	LC _{stems}	LC _{reprod}	LC _{Total}
RC _{<4.0}	0.04	0.20	0.72*	0.80**									
RC _{4.0-20}	-0.13	0.02	0.84**	0.89**									
RC _{<20}	-0.13	0.02	0.84**	0.89**									
RC _{>20}	0.31	-0.28	0.17	0.17									
RC _{Total}	0.21	-0.10	0.47	0.48									
LC _{leaves}	0.05	0.42	0.53(*)	0.58(*)	0.73**	0.79**	0.79**	0.46	0.64*				
LC _{stems}	-0.12	-0.57(*)	0.72*	0.71*	0.43	0.59*	0.59*	0.08	0.30				
LC _{reprod}	0.41	-0.50(*)	0.43	0.28	0.31	0.35	0.35	0.41	0.57(*)				
LC _{Total}	-0.08	-0.44	0.78**	0.74**	0.56(*)	0.76**	0.76**	0.35	0.55(*)				
SC ₀₋₅	0.22	-0.67*	0.67*	0.55(*)	0.24	0.36	0.36	-0.10	0.14	-0.03	0.60*	0.49	0.51(*)
SC ₅₋₁₀	0.47	-0.57(*)	0.66*	0.54(*)	0.35	0.41	0.41	0.09	0.24	0.10	0.51(*)	0.54(*)	0.51(*)
SC _{Total}	0.33	-0.62*	0.66*	0.55(*)	0.34	0.43	0.43	0.04	0.24	0.08	0.57(*)	0.53(*)	0.54(*)

Table S3.4. Observed stock changes in carbon associated to aboveground biomass of trees during 3yr periods in secondary and old growth tropical dry forests in the Chamela-Cuixmala region, western Mexico. All the values are in Mg C ha⁻¹ 3yr⁻¹.

Site	Cr0	Za0	Ma1	Ra3	Ca4	Cr5	Ra10	Ca12	Cr12	Gar	Tej1	Tej2
Forest age in 2004	0	0	1	3	4	5	10	12	12	OGF	OGF	OGF
2004-2007 period	-0.33	3.09	3.33	2.69	4.46	-1.17	-1.33	2.5	1.55	3.21	-0.71	-0.67
2007-2010 period	2.02	2.05	4.71	7.14	4.97	3.68	0.42	4.43	2.38	1.28	1.87	2.13

Table S3.5. Parameters and statistics of chronosequence models to test the effects of forest age on tree aboveground biomass C (ABC_T) and the observed changes through time (dABC_T) in nine secondary tropical dry forest and three old-growth forest sites in the Chamela-Cuixmala region, western Mexico. A logistic model was fitted to ABC_T: $ABC_T = (a/(1 + e^{((b-t)/c)}))$. Its first derivative was fitted to dABC_T: $dABC_T = (ae^{((b-t)/c)}/c)/(1 + e^{((b-t)/c)})^2$. Response refers to the variable evaluated and the year or period is indicated in parenthesis. RSE: residual standard error. R²: coefficient of determination. Parameters in bold correspond to the test of the effect of forest age on the variables. ** $P < 0.01$, * $P < 0.05$, (*) $P < 0.1$, ns: non-significant.

Response	a	b	c	RSE	R ²
ABC _T (2004)	27.79**	9.72**	3.42**	2.47	0.96
ABC _T (2007)	28.53**	12.12**	4.16**	2.19	0.97
dABCT (2004-2007)	17.10ns	2.25ns	1.02ns	0.07	0.19
dABC _T (2007-2010)	67.10**	7.61ns	3.35**	1.94	0.16

Capítulo 4. *Aboveground carbon - diversity association across a transformed tropical dry forest landscape: implications for the implementation of REDD+*

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In preparation

Abstract

The conservation of biological diversity through the implementation of a mechanism for reducing greenhouse gases emissions from deforestation and forest degradation (REDD+) depends upon the selection of adequate target sites and forest management activities. Assessments of how carbon (C) and biodiversity are associated across space and the factors affecting such association represent a tool to improve such selection. Here we evaluate how are aboveground C stocks in tree biomass (ABC_T) and tree diversity related in a human-modified tropical dry forest landscape in western Mexico. We assessed such association at both site and landscape levels based on forest censuses conducted at 50 locations across the landscape, which included both secondary and old growth forests under management. At site level, scatterplots were drawn to identify different ABC_T -diversity combinations for REDD+ implementation. We informed such association by mapping into those scatterplots the effect of forest age, topography, previous land use, and landscape configuration on ABC_T and diversity derived from regression tree analyses. At the landscape level, we simulated the effect of different landscape deforestation scenarios on cumulative ABC_T and species diversity maintenance. We found that at site level, forest age was the main driver of ABC_T and species diversity. ABC_T in secondary forests was negatively associated with the duration of previous land use, and species richness and composition were affected by the type of previous land use and the proportion of the landscape under agricultural activities. Such effects influenced the ABC_T -diversity relationship. Both C and diversity were maximized almost exclusively in old growth forests; species diversity peaked in some secondary forests but not C stocks, while very few secondary forests maximized C stocks. At the landscape level, reductions in ABC_T were largest when deforestation concentrated on old growth forests, while the largest reduction in species richness and a more profound modification in species composition arose when concentrated on young secondary forests. Our results suggest that beyond old growth forests, secondary forests in an advanced successional stage also have high potential for REDD+ implementation, because of their intermediate C stocks, their high species diversity and their additional carbon capture potential. Other secondary forests could be included only if their carbon capture potential is enhanced through active restoration, if productive practices are modified, and if safeguards are designed to prevent deforestation leakage.

Introduction

Payment for the reduction of greenhouse gases emissions from deforestation and forest degradation in developing countries (REDD+) has been proposed as one of the main mechanisms for climate change mitigation, due to its apparently cost-effectiveness and its potential to reduce emissions in the short term. Potential co-benefits of REDD+ implementation, for which the “+” sign stands for, include poverty reduction, improved forest governance on resources, and biodiversity conservation (Angelsen, 2008; Parrotta *et al.*, 2012). Biodiversity co-benefits have commonly been framed within a “win-win” perspective: REDD+ targeted areas should be those with both the highest carbon stocks and the highest biodiversity. Assessments at global scales have shown that such scenarios exist (UNEP-WCNC, 2008; Strassburg *et al.*, 2010), but the strength of the association between carbon stocks and diversity declines at more local spatial scales and when data of higher spatial resolution are used (Egoh *et al.*, 2009; Chisholm *et al.*, 2013). Furthermore, there is a trade-off between reducing emissions and conserving biodiversity, since deforestation hotspots do not overlap with biodiversity hotspots (Venter *et al.*, 2009; Paoli *et al.*, 2010).

A broader spectrum of areas for REDD+ implementation could be considered if their carbon and diversity benefits and trade-offs were explicitly recognized, which would allow the identification of adequate management interventions or financial options (Phelps *et al.*, 2012a, 2012b). For example, undisturbed biodiversity-rich areas with moderate carbon benefits for REDD+ could be included under a co-financing scheme for biodiversity protection (Venter *et al.*, 2009; Phelps *et al.*, 2012a). Previously degraded areas of moderate biodiversity and C value, such as logging impacted areas, or secondary forests growing on previous agricultural lands could be targeted for REDD+ if management activities aimed at enhancing C stocks and diversity were implemented (Edwards *et al.*, 2011; Pichancourt *et al.*, 2014). Recognizing those carbon-diversity scenarios seems therefore crucial for the adequate selection of both forest management activities and financing schemes that would result in increased outcomes (Parrotta *et al.*, 2012; Phelps *et al.*, 2012a), although the selection depends also on the socioeconomic context (Phelps *et al.*, 2012b; Balderas Torres *et al.*, 2013; Skutsch *et al.*, 2013).

In tropical landscapes, human activities, commonly (but not restricted to) timber extraction and forest clearance for agricultural purposes, and the subsequent dynamics of such transformed areas, have created a mosaic of patches of different plant cover types, whose carbon stocks and species diversity may depend on both abiotic factors and human use (Hernández-Stefanoni *et al.*, 2010; Gibson *et al.*, 2011; Berenguer *et al.*, 2014). This is particularly true for secondary forests, which commonly accumulate biomass and species as they grow (Becknell *et al.*, 2012; Martin *et al.*, 2013; van Breugel *et al.*, 2013), although

accumulation rates and similarity to old-growth forests depend on biophysical conditions and their use history (Molina Colón y Lugo, 2006; Becknell *et al.*, 2012; Williamson *et al.*, 2012; Jakovac *et al.*, 2015). Since secondary forests have become major components of tropical landscapes (Wright, 2005; Foley *et al.*, 2007; FAO, 2010), understanding the association between carbon stocks and species diversity in those landscapes implies their inclusion in forests assessments. Also, the recognition of their biophysical and human drivers could inform the selection of forest management activities attempting to conserve or increase their carbon stocks and diversity under a REDD+ implementation scenario.

In this study, we quantified the association between aboveground C stocks in living tree biomass (ABC_T) and tree species diversity across a tropical dry forest landscape modified by human activities, and where secondary forest and old growth managed forest are significant components of the landscape. We assessed such association at both site and landscape levels. At site level, we informed such association by assessing the role of forest age, topography, land use history, and landscape configuration on both C stocks and species diversity. At the landscape level we assessed the effect of different landscape transformation scenarios on the cumulative C stocks and species diversity. The three particular objectives of the study were: (1) to identify which are the main factors explaining variation in C and species diversity at site level, (2) to assess the C-diversity relationship at site level and how it is mediated by such factors, and (3) to assess the C-diversity relationship at the landscape level and how it is mediated by different landscape deforestation scenarios. Through this assessment, we aimed to provide guidelines on how to manage a human modified tropical dry forests landscape under a REDD+ scheme implementation that could generate both C and biodiversity benefits.

Materials and methods

Study region

The study was conducted in the Chamela-Cuixmala region, on the Pacific coast of the Jalisco State, Mexico (19°23' - 19°42'N, 104°48' - 105°11'W). Mean annual temperature is 24.6 °C. Mean annual precipitation over the 1983-2013 period was 756 mm, concentrated between June and October (data from the "Watershed Project", UNAM). The region was mostly covered by tropical dry forest (TDF) on hills, and by tropical semi evergreen forests (TSEF) in the valleys along the main rivers and temporal streams (Durán *et al.*, 2002); these

two forests types originally accounted for ca. 89 % y 11 % of the landscape, respectively (Castillo *et al.*, 2005). In the central part of the region is the Chamela-Cuixmala Biosphere Reserve (CCBR), a 13.142 ha area located mostly on private lands and devoted exclusively to conservation and scientific research (Ceballos y García, 2010). Modern human settlement in the region began in the 1970's (Castillo *et al.*, 2005). Since then, forest has been transformed mainly by slash-and-burn into croplands on valleys and into pastures for livestock production on hills. Agricultural areas are maintained through repeated cultivation, while pastures are commonly maintained through periodical slashing of the woody vegetation and burning (Trilleras *et al.*, 2015). However, because of reduced productivity or changes in regional socioeconomic conditions, agricultural or pasture maintenance practices can be reduced or suppressed, which results in the development of secondary vegetation (Burgos y Maass, 2004). Forest (both old-growth and secondary) is also subjected to non-clearance management, including the extraction of timber and non-timber products and cattle browsing (Burgos y Maass, 2004; Rendón-Carmona *et al.*, 2009; Cohen, 2014). By 2004, around 80 % of the region was covered by old-growth or secondary TDF, 16 % was agricultural land and pastures, and only 2 % represented secondary or old-growth TSEF (Sánchez-Azofeifa *et al.*, 2009).

Site selection

Fifty sites were selected across the Chamela-Cuixmala region to represent major gradients in biophysical and land use conditions known to cause major variations in aboveground C stocks and species diversity, but restricted by owner's willingness to allow for forest measurements and for providing information on previous land use. Those gradients were: forest age, topographic position, and previous land use.

Forest age. ABC_T and species diversity commonly increase as secondary forests age in TDF landscapes (Hernández-Stefanoni *et al.*, 2010; Becknell *et al.*, 2012; Mora *et al.*, 2015). Therefore we selected both old growth (with no record of clearing) forests and secondary forest sites across all the range of forest age spanned in the region (5-45 yr). Forest age was determined through interviews with landowners. The last year of at least one of the management activities used for pasture maintenance (slashing, burning, or herbicide application, see Trilleras *et al.*, 2015) was defined as the year since which forest age was calculated. For those forests less than 10 yr old, age was confirmed by inspection of satellite images available in Google Earth® (the earliest from 2003-2004).

Topography. Larger C stocks and a different species composition has been found in TSEF associated to valleys than in TDF on hills across the old-growth forests landscape of the

Chamela-Cuixmala region (Balvanera *et al.*, 2002; Jaramillo *et al.*, 2003a). Therefore, these two contrasting topographical positions, hills and valleys, were distinguished. Valleys included both alluvial terraces and piedmonts, whereas hills included slopes and hilltops.

Land use history. Previous land use and management, as measured by the type, magnitude, frequency, and length of the activities related to it, have been shown to affect C stocks and diversity recovery along succession (Uhl *et al.*, 1982, 1988; Hughes *et al.*, 1999; Zarin *et al.*, 2005; Williamson *et al.*, 2012; Orihuela-Belmonte *et al.*, 2013; Jakovac *et al.*, 2015). We characterized these main aspects of land use in the region that could affect C stocks or species diversity following previous assessments (Burgos y Maass, 2004; Trilleras *et al.*, 2015). Through interviews with landowners, a timeline was established for each site, along which major use activities were characterized (Table S4.1). For non-cleared sites, main aspects referred to the magnitude, frequency and length of extractive activities (timber extraction, stakes extraction), or livestock production. For previously cleared sites, additional information on the use between clearance and forest regrowth was assessed. This included the type of clearing (by slash and burn or bulldozer), main use after clearing (agriculture, pasture or both), the frequency and length of management activities during main use (cultivation, slashing, burning, or herbicide application), and use after such main use ceased and secondary succession began (as characterized for non-cleared forests).

Site characterization

Additional topographic characteristics were recorded at each site (Table S4.1). Aspect was measured using a compass. Mean slope and elevation were derived from five elevation measurements taken at regular intervals along the site's main axis (Figure S4.1) using a Garmin® eTrex 20® GPS device. Landscape configuration was also characterized by analyzing satellite imagery from Google Earth® Plus. Three different land cover types (agriculture lands, pasture lands, and forests) were defined and their relative contribution within a 1 km buffer around each site quantified. Forested areas were further subdivided into < 10 yr and > 10 yr forests by reviewing the series of historical satellite images available (the earliest one being from 2003-2004). Images were analyzed using Google Earth® Plus.

Vegetation sampling

Vegetation sampling followed two different protocols. In 38 sites we followed a sampling protocol modified from Baraloto *et al.* (2013). At each site an 80-m long compass line was established running downslope in hilly sites or with a north direction in valleys.

Perpendicular to this line, five 5 × 50 m plots were laid down at 15-m intervals; adjacent plots ran in opposite directions from the major axis (Figure S4.1a). Within each plot, a stratified sampling was used. Stems ≥ 10.0 cm diameter at breast height (DBH) were measured in the entire plot (5 × 50 m), while stems with 5.0 ≤ DBH < 10 cm DBH were measured within a nested 2 × 50 m plot. Measurements were made in January and April 2013, and between December 2013 and January 2014. An additional set of 12 sites, included in a long-term research project on successional dynamics (Martínez-Ramos *et al.*, 2012) were sampled. At each site a 30 × 60 m plot was established and a stratified sampling was followed (Figure S4.1b). Stems ≥ 10.0 cm DBH were measured in the entire plot (30 × 60 m), while stems with DBH ≥ 5.0 cm were sampled in a 20 × 50 m subplot. Measurements were taken between September and October 2013.

Carbon stocks and species diversity estimation

We estimated aboveground biomass C in trees (ABC_T), defined as the C stored in woody live trunks and stems of trees above the soil surface. ABC_T was estimated from tree measurements by applying a local allometric equation that includes DBH and wood density as predictors (Martínez-Yrizar *et al.*, 1992); we did not use an allometric equation with height as a predictor variable, because we had no such information for each individual stem. Wood density values of the species were obtained from published and unpublished data for Chamela (Barajas-Morales, 1985, 1987; Martínez-Yrizar *et al.*, 1992). When site data were not available, species values from other locations or mean values for the genus were used (Chave *et al.*, 2006). For species with no available information, a mean community value was assigned. ABC_T were estimated by multiplying biomass by a conversion factor of 0.48 (Jaramillo *et al.*, 2003a). Lianas and cacti were not included in ABC_T estimates because of the lack of allometric equations for these life forms in TDF; however, cacti account for 0 to 17 % (median = 0 %) of the basal area across all sites. Because of the nested sampling design, ABC_T was estimated independently for the two size categories (5.0 to 9.9 cm and ≥ 10 cm DBH) to constant area (1 ha) and then added to obtain ABC_T .

Two components of tree species diversity were evaluated: species richness and species composition. Species richness was estimated following a rarefaction-like procedure. Rarefaction is a technique that allows for the estimation of the expected number of species in a site given a standardized number of individuals, allowing for a direct comparison of sites with different individual density or sampled with different protocols (Gotelli y Colwell, 2001). We implemented a carbon-based rarefaction, so that rarefied richness represents the expected number of species holding ABC_T constant across all sites (120 kg of C). This

approach weights the addition of new individuals by the biomass of the species to which they belong. Rarefaction was implemented using 'rarefy' function in the vegan library for R (Oksanen *et al.*, 2011). Species composition was transformed to a continuous scale by performing a non-metric multidimensional scaling ordination (NMDS) to a matrix of species ABC_T values per site. The Bray-Curtis dissimilarity distance was used. Site scores on the first two ordination axes were used as measures of species composition (called axis A and B). The analysis was performed using the 'metaMDS' function in the vegan package for R (Oksanen *et al.*, 2011).

Factors explaining variation in C stocks and species diversity across the landscape

A regression tree analysis was performed to explore the effect of forest age, topography, land use history, and landscape configuration on ABC_T , species richness and species composition. Although not a hypothesis testing procedure, regression trees provide a good approximation to the variables in a dataset explaining variation in a response variable, especially when multiple potential predictors are assessed, their effects are present only for some portion of the data set, or when they are quantifiable or meaningful only for a subset of the data (Venables y Ripley, 2002; Myatt, 2007). A total of 28 variables were included as predictors in the analysis (Table S4.1). Regression trees were fitted using the function 'rpart' for R (Therneau *et al.*, 2014). Optimal tree size was determined using cost-complexity pruning based on 10-fold cross-validation (Venables y Ripley, 2002). The particular effects identified through regression tree analysis were then tested using linear and non-linear models. ABC_T and species diversity categories derived from regression tree analysis were used in further analyses.

C-diversity relationship at site level

Scatterplots of ABC_T and species richness or ABC_T and species composition were drawn and Spearman correlations were calculated to assess the degree of association between those variables at the plot level. We then defined the low, medium and high values of both ABC_T and diversity by splitting their ranges into three equal intervals each. Taking those subdivisions into the ABC_T -diversity scatterplots allowed us to define the main nine ABC_T -diversity combinations present across the landscape (e.g. low ABC_T -high species diversity). Finally, we mapped ABC_T and species diversity categories derived from regression trees onto these ABC_T -diversity scatterplots to qualitatively assess how site conditions (forest age,

topographic position, land use history, and landscape configuration) influence the location of particular sites within the scatterplots and therefore the C-diversity relationship.

C-diversity relationship at the landscape level

Since the main aim of implementing a REDD+ program is the reduction of C emissions from deforestation and forest degradation relative to a baseline level, assessing its impact requires a landscape- or regional-level accounting of its benefits. To assess such potential benefits of conserving both C stocks and biodiversity, we simulated how ABC_T and tree species diversity would be conserved at the landscape level under different deforestation scenarios. We however did not seek to provide a forecasting of landscape spatial configuration or to provide an accurate picture of the C stocks and species diversity values in the future, since our simulations were not spatially explicit nor do they include explicitly the effects of previous or projected land use characteristics at each site within the landscape.

The first step of the simulation consisted in setting the initial condition of the landscape. We defined the landscape as 100,000 ha area, which approximates to the total area within which our 50-sites sample was taken. The landscape was subdivided into 1 ha plots and each plot was assigned a topographic position and an initial land cover. Topographic position had two possible values: hills and valleys. Land cover had four possible categories, agricultural or active pasture lands plus three different forest types derived regression tree analysis: young (≤ 18 yr), intermediate ($18 < \text{age} \leq 40$ yr), and old (> 40 yr together with old-growth forests). The initial landscape land cover condition was derived from the 2005 land cover estimates for the region (Sánchez-Azofeifa *et al.*, 2009) and our own estimates of different forest types. The relative assignation of plots to each topographic and land cover combination can be found in Table S4.2. ABC_T and a tree community composition were assigned randomly to each plot based on the forest type and topographic position to which they were assigned. ABC_T values for each plot were assigned randomly from normal distributions of ABC_T with mean and standard deviations for each land cover and topographic condition calculated from our 50 site sample. Tree community was also assigned randomly to each plot based on its topography and land cover category using the 'rrarefy' function in the vegan package for R (Oksanen *et al.*, 2011).

Simulations consisted in the random selection of plots under forest coverage and their transformation to agricultural or pasture lands. We settled 28 different deforestation scenarios, for which both ABC_T and species diversity at the landscape level were estimated after the simulation proceeds. Deforestation scenarios were derived from the combination

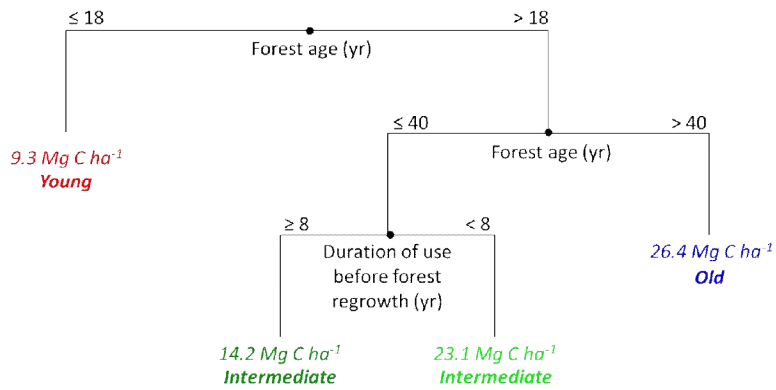
of different deforestation levels and treatments. Seven deforestation levels were settled: 0 %, 25 %, 50 %, 75 %, 100 %, 125 % and 150 % of the baseline scenario. The baseline scenario was defined as the net deforestation level through the 1970-2005 period (9 % and 82 % of the original landscape for hills and valleys in 35 years, respectively, assuming deforestation in the region began around 1970, see Castillo *et al.*, 2005; Sanchez-Azofeifa *et al.*, 2009). Therefore, our simulation encompasses a period of 35 years from 2005 (*i.e.* a “2040 projection”). Four deforestation treatments were defined based on their potential effects on ABC_T : (1) the same deforestation probability for the three forest types, (2) all the deforestation occurring in the old forests type, (3) all the deforestation occurring in the intermediate forest type, and (4) all the deforestation occurring in the young forest type. When no enough forest cover existed under a particular forest type to account for the implied deforestation level, deforestation was transferred to the other forest types within the same topographic position. Ten simulations were run for each deforestation scenario. Simulations were run using R (R Development Core Team, 2011).

Results

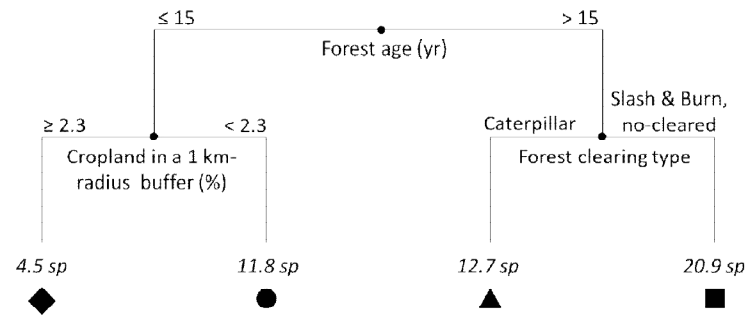
Variation in C stocks and species diversity in relation to forest age, topography, land use history and landscape configuration

Forest age was the main variable explaining differences in C stocks and species diversity across sites. Forest age was the first criteria for splitting the data in regression trees (Figure 4.1a-c), with the exception of NMDS axis B scores (Figure 4.1d). Forest age was involved in further tree ramifications in the case of ABC_T and species composition (Figure 4.1a,c). Previous land use explained differences in C stocks and species richness among sites (Figure 4.1a,b), while landscape configuration explained further differences in species richness and species composition (Figure 4.1b,c). Topographic position was also a main factor explaining differences in species composition among sites (Figure 4.1d).

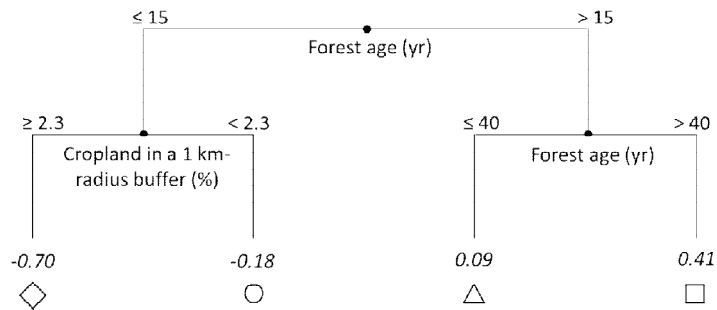
a) ABC_T stock



b) Species richness



c) Species composition axis A



d) Species composition axis B

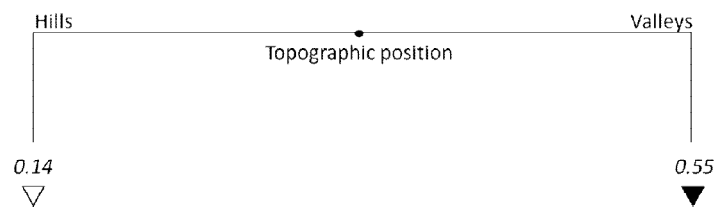


Figure 4.1. Regression trees assessing the effect of forest age, topographic position (hills and valleys), previous land use and landscape configuration on site aboveground living biomass C stocks (a), tree species richness (b), and tree species composition (c, d) across secondary and old growth forest in the Chamela-Cuixmala region. Predictor variables are depicted just below each branching node, and their thresholds values on each branch. The mean value for the variable analyzed is reported below each terminal branch, together with the color or symbol character used to identify the branch in further figures.

C stocks were mainly explained by forest age. ABC_T varied between 0.1 and 36.3 Mg C ha⁻¹, increasing with age following a slightly sigmoid pattern (Figure 4.2a); forest age explained 54.4 % of the variance. Three ABC_T categories were defined from regression tree analysis based on the effect of forest age alone: “young” forests, those with ≤ 18 yr, have a mean ABC_T stock value of 9.3 Mg C ha⁻¹, “old” forests, including secondary forests > 40 yr and non-previously cleared (old growth) forests, with a mean C stock of 26.4 Mg C ha⁻¹, and “intermediate” forests, which include sites with ages between 19 and 40 yr (Figure 4.1a). For intermediate forests, the length of use for agricultural activities before forest regrowth had an effect on ABC_T ($F = 5.2$, $df = 1$, $P < 0.05$, Figure 4.2b), with sites used for more than eight years having a mean C stock value of 14.2 Mg C ha⁻¹, while those used a shorter period having a mean stock value of 23.1 Mg C ha⁻¹. A total of four ABC_T categories resulting from the joint effects of forest age and length of use were therefore identified (Figure 4.1a, Figure 4.2a,b). The inclusion of stems $2.5 \leq DBH < 5.0$ cm increased the C stock values, particularly for the young forests sites, although the association with forest age was not modified (Figure S4.2).

Species richness was jointly explained by forest age, landscape configuration and land use. Rarefied species richness increased asymptotically with forest age (Figure 4.2c), which explained 37.5 % of its variation. Two main site categories were defined from the effect of forest age: sites ≤ 15 yr and those > 15 yr (Figure 4.1b). Sites < 15 yr and located in landscapes where agriculture lands comprise at least 2.3 % of the landscape in a 1-km radius buffer had fewer species (mean rarefied richness = 4.5 sp) than those surrounded by less agricultural land (mean rarefied richness = 11.8 sp; $F = 15.5$, $df = 1$, $P < 0.01$; Figure 4.1b, Figure 4.2d). On the other hand, sites > 15 yr and cleared with bulldozer had fewer species (mean rarefied richness = 12.7 sp) than those cleared with slash-and-burn or never cleared (mean rarefied richness = 20.9 sp, $F = 6.7$, $df = 2$, $P < 0.01$; Figure 4.1b, Figure 4.2e). From the interaction between forest age, landscape configuration, and land use history effects, four species richness categories were identified (Figure 4.1b, Figure 4.2c-e).

Species composition was explained by forest age, landscape configuration and topography. Scores on the NMDS axis A showed an increasing pattern with forest age (Figure 4.2f), which explained 37.7 % of the variation. Three species composition categories were derived based on the effect of forest age on NMDS axis A (Figure 4.1c): sites > 40 yr (including old growth forests), with a mean axis A value of 0.41, sites 15-40 yr, with a mean axis A value of 0.09, and sites with ≤ 15 yr. Those sites were further grouped based on the proportion of agricultural land surrounding them. Sites located in landscapes where agriculture lands comprise at least 2.3 % of the landscape had lower scores (mean axis A value = -0.71) than those surrounded by less agricultural land (mean axis A value = -0.18; $F =$

6.3, $df = 1$, $P < 0.05$, Figure 4.2g). A total of four composition axis A categories resulting from the joint effects of forest age and landscape configuration on species were defined (Figure 4.1c, Figure 4.2f,g). NMDS axis B scores were not related to forest age (Figure 4.1d), but revealed a clear distinction in species composition between sites on hills and those on valleys ($F = 45.5$, $df = 1$, $P < 0.01$, Figure 4.1d, Figure 4.2h).

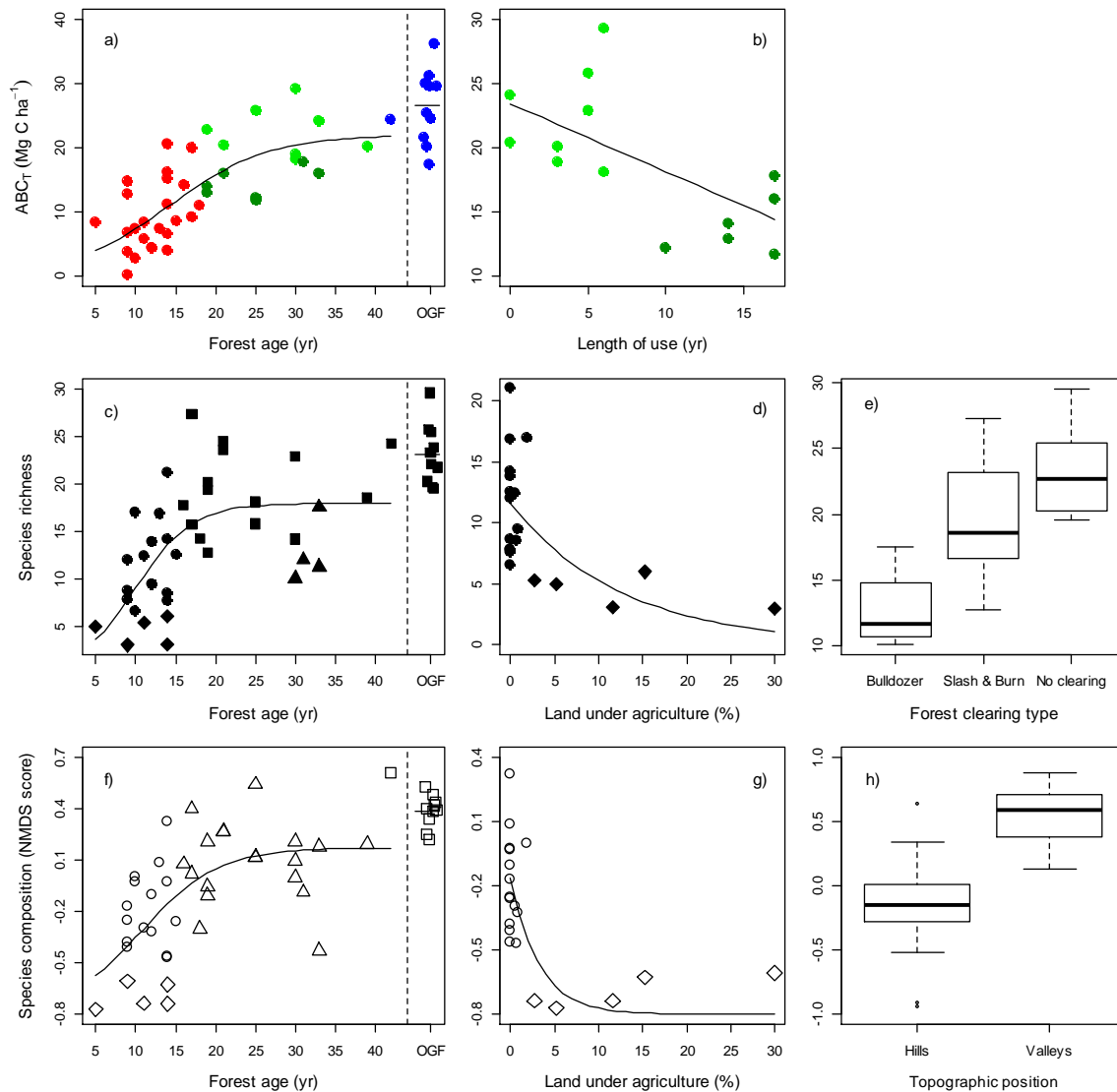


Figure 4.2. Statistically significant relationships between aboveground biomass C in trees (ABC_T , upper panels), rarefied species richness (mid panels), species composition (lower panels) and forest age, topography, previous land use and landscape configuration variables derived from regression tree analysis. Panels f-g correspond to species composition axis A, while panel h corresponds to composition axis B. Continuous lines in panels a-d and f-g represent fitted models. All the relations shown were statistically significant ($P < 0.05$). Colors and symbols are derived from Figure 4.1. OGF: old growth forests.

Carbon-diversity relationship at site level

At site level, species diversity was positively associated to C stocks. Both species richness and species composition axis A scores were significantly correlated to ABC_T ($\rho = 0.62$, $P < 0.001$ for rarefied richness; $\rho = 0.59$, $P < 0.001$ for composition Axis A; Figure 4.3 a,b). Scores of species composition axis B showed no relation with ABC_T ($\rho = -0.13$, $P = 0.36$, Figure 4.3c).

C stocks were maximized in old forests. Eight out of 10 sites within the upper third of the ABC_T values belong to the old forests category, with two additional sites being intermediate forests (panels 7-9 within Figure 4.3a,b). Species richness was maximum in old forests (eight sites), although also in young and intermediate forests (five sites, see panels 1,4,7 in Figure 4.3a). Species composition showed a larger number of sites maximizing its value. All the 11 old forests plus nine secondary forests, mostly intermediate, were included in the upper third values of NMDS axis A (panels 1,4,7 in Figure 4.3b). ABC_T and species diversity were greatest in old forest only (panel 7 in Figure 4.3a,b).

Intermediate forests, particularly those with a shorter use period previous to regrowth, also tended to have high C stocks, species richness, and a very similar composition than old forests (Figure 4.3a,b). Those sites were mostly located at the mid third of the C stocks range and in the upper two-thirds of species richness and species composition values (Panels 4-5 in Figure 4.3a,b). Within them, sites cleared with bulldozer had lower species richness (panel 5, Figure 4.3a; see also the triangle within panel 9).

On the contrary, young secondary forests sites had the lowest C stocks and intermediate to low levels of species diversity. All but one of the sites in the lower third of ABC_T values observed were young forests (panels 1-3 in Figure 4.3a,b). A few, additional set of such sites were in the mid third of ABC_T values, but within the lowest range of species richness and species composition values (panel 6 in Figure 4.3a,b). Particularly noticeable were those sites within a landscape with a high proportion of agricultural lands, which had lower species richness and NMDS axis A scores given their ABC_T values (diamonds in Figures 4.3a,b).

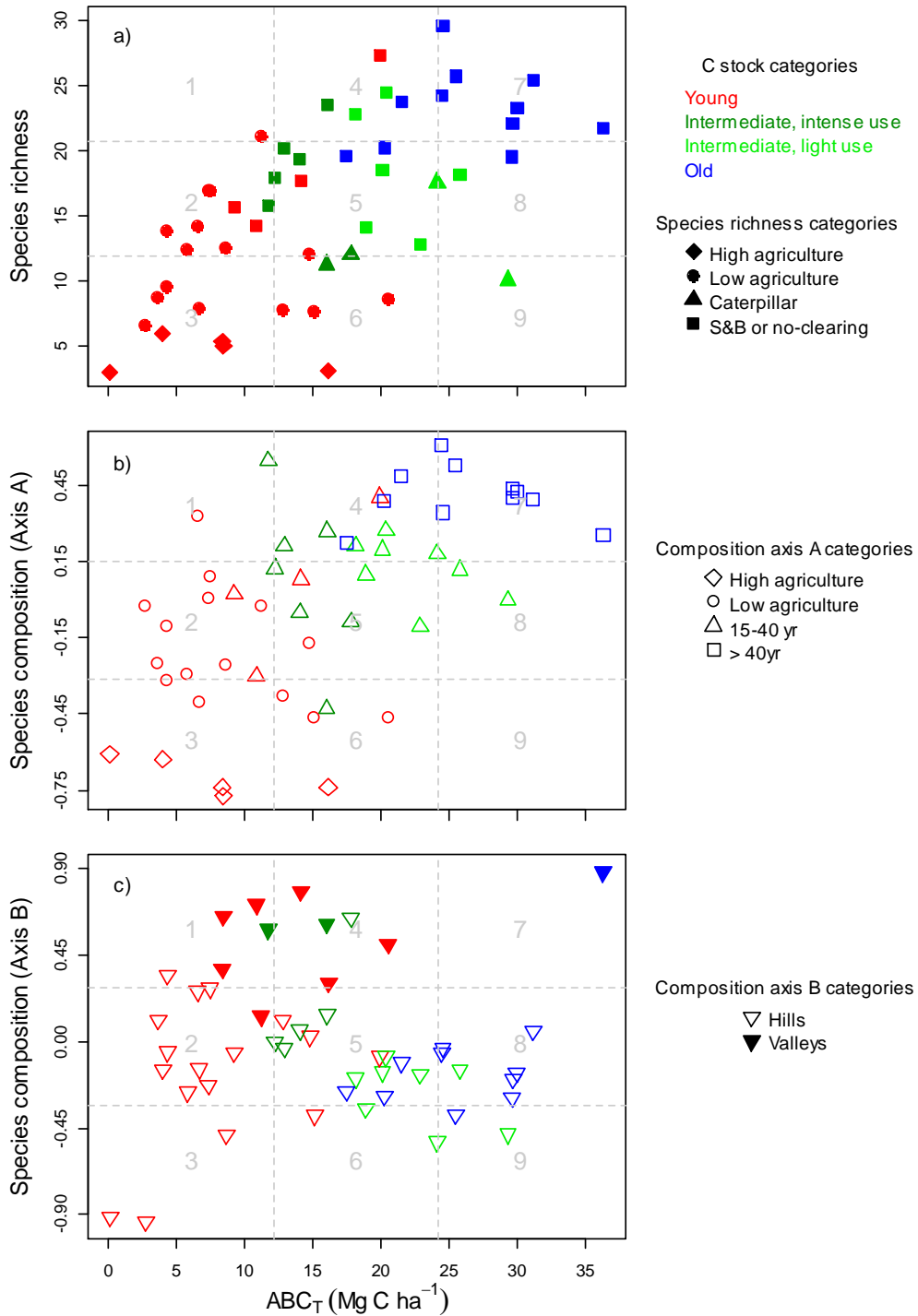


Figure 4.3. Site-level association between tree aboveground living biomass (ABC_T) and the rarefied species richness (a) and species composition (b,c) of the tree community. Dotted lines divide the scatterplot into nine areas (numbered 1 to 9) of equal ABC_T and species diversity amplitude. Species composition was measured through the first two axes of a non-metric multidimensional scaling ordination (NMDS). Point characters and colors indicate categories derived from regression tree analyses (see Figure 4.1).

Carbon-diversity relationship at the landscape level

As expected, landscape ABC_T and species richness showed reductions with increasing deforestation level, but such reductions differed between deforestation treatments (Figure 4.4a). Given the same deforestation level, ABC_T reduction was largest when deforestation occurred exclusively in old forests, intermediate (and very similar) when occurred in intermediate secondary forest or evenly distributed across forest types, and lowest when happening in young forests. Reductions in species richness followed an opposite pattern. Given the same deforestation level, the largest reduction in species richness was found when deforestation occurred in young forests and the lowest when it happened in old forests; an evenly distributed deforestation across forest types reduced the loss of species when compared to a deforestation occurring on intermediate forests (Figure 4.4a).

The axes of species composition displayed contrasting patterns in relation to deforestation treatment. NMDS axis A scores tended to decrease both as deforestation increases in magnitude and as it concentrates on forests with higher C stocks (Figure 4.4b). Conversely, NMDS axis B scores showed that when deforestation occurred in old forests, smaller and opposite changes occurred than when it occurred in forests with lower C stocks (Figure 4.4c). Evenly distributed deforestation across forest categories resulted in the lowest divergence in NMDS axis B scores relative to the initial simulation values (*i.e.*, no deforestation).

Only when deforestation levels were above those of the baseline scenario (*i.e.*, > 100 %), and occurred only in old forests, landscape ABC_T values were reduced below the baseline limit defined from the 1970-2005 period (Figure 4.4). Also, the largest reduction in ABC_T and species richness values among adjacent deforestation levels occurred between 0 % and 25 % deforestation scenarios, no matter which deforestation treatment is followed (Figure 4.4a).

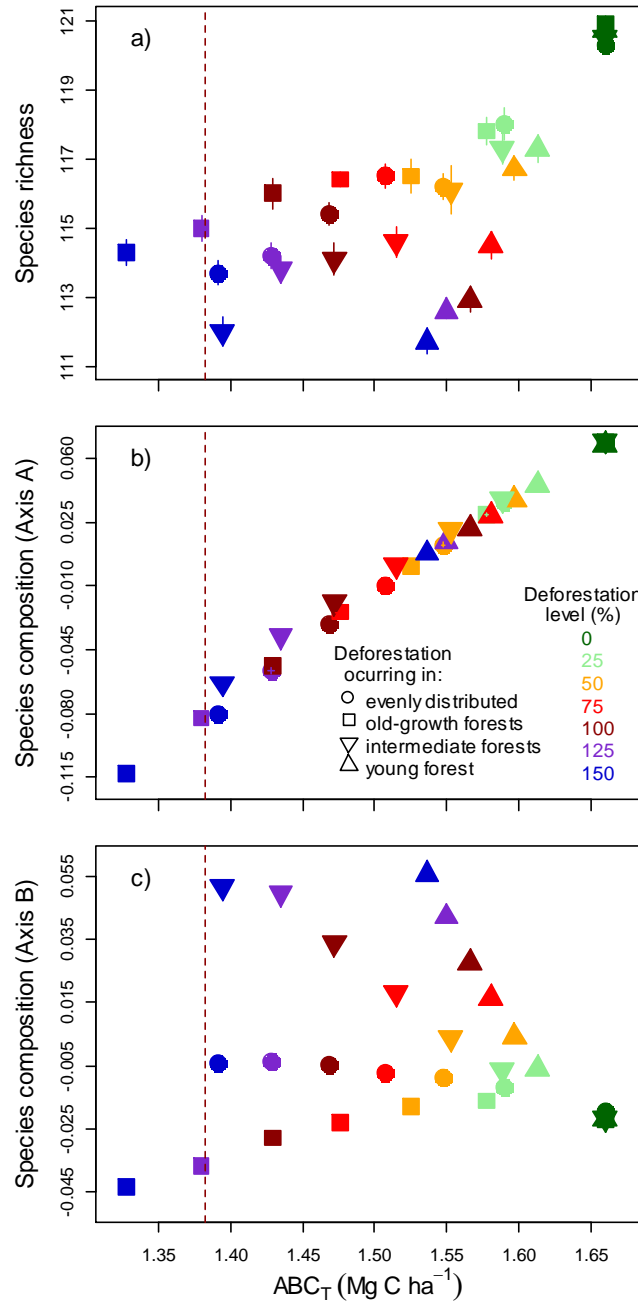


Figure 4.4. Landscape-level association between tree aboveground living biomass (ABC_T) and the species richness (a) and species composition (b, c) of the tree community derived from deforestation simulations. Simulations proceed from an initial condition of the landscape in 2005 (dark green symbols) through increasing deforestation levels (indicated by colors) for different deforestation treatments (indicated by symbols). For each combination of deforestation treatment and level, landscape ABC_T and total species diversity or species composition was calculated. Dotted lines represent the baseline scenario, *i.e.*, the expected landscape ABC_T level if deforestation would have been the same that under the precedent 35 yr baseline period (1970-2005). Species composition was measured through the first two axes of a non-metric multidimensional scaling ordination (NMDS). Vertical and horizontal lines on symbols indicate ± 1 standard error.

Discussion

Factors explaining variation in aboveground carbon stocks and species diversity at site level

Our results on the factors explaining variation in C stocks and species diversity are in general agreement with previous reports from other tropical dry regions. Similar assessments in human modified landscapes have shown that forest age is one of the most important factors (if not the main) explaining C stocks and species diversity, as found here (Ruiz *et al.*, 2005; Vargas *et al.*, 2008; Hernández-Stefanoni *et al.*, 2010; Lebrija-Trejos *et al.*, 2010a; Becknell *et al.*, 2012; Mora *et al.*, 2015). Yet, beyond the forest age effect several other factors contribute to explain such variation. We found that higher impact clear-cut methods, like the use of bulldozer, and the duration of use before forest regrowth, impacted negatively on the recovery of C stocks and species richness. Previous work has also documented such effects both in the dry (Uhl *et al.*, 1982; Molina Colón y Lugo, 2006; Romero-Duque *et al.*, 2007; Eaton y Lawrence, 2009) and wet tropics (Uhl *et al.*, 1988; Hughes *et al.*, 1999; Zarin *et al.*, 2005; Orihuela-Belmonte *et al.*, 2013; Jakovac *et al.*, 2015). However, our analysis shows that such effects could be evident only for certain periods of forest regrowth, *i.e.*, the effect of previous land use may interact or be dependent upon forest age. Longitudinal studies of successional forest support this assertion, since some of the initial effects of differential land use may occur only at initial stages of succession, disappearing afterwards (Mesquita *et al.*, 2001; Williamson *et al.*, 2012). It is also highly possible that the disturbance regime of tropical forests has changed through time (Lawrence *et al.*, 2007; Eaton y Lawrence, 2009; Jakovac *et al.*, 2015), making the effects of different land use components apparent only for certain age ranges. This is certainly the case for the mechanized clearing of forest, very common in the study region during the 1970's to 1980's due to governmental promotion (Castillo *et al.*, 2005), but mostly absent thereafter.

Interestingly, an increased proportion of land under agriculture is associated to reductions in species richness and composition recovery. Previous studies in other tropical regions have shown that a reduced forest cover in the landscape relates to reduced diversity in secondary forests, attributing this effect to reduced propagule dispersal (Cubiña y Aide, 2001; Jakovac *et al.*, 2015). However, in the case of the Chamela-Cuixmala region, increased cropland cover may be related to increased use of adjacent secondary forests. Agriculture in this landscape is practiced only in valleys associated to the arroyos and main rivers (Burgos y Maass, 2004; Cohen, 2014). The hilly areas surrounding them may be more prone to be used more frequently for raising cattle, sustaining higher stock densities, or

being more frequently burned (Burgos y Maass, 2004), although we did not detect such direct effects, probably because of our reduced sample under such conditions.

Larger C stocks in valleys were expected both in old growth and secondary forests, in association with the higher soil water moisture content and nutrient availability (Cotler *et al.*, 2002; Jaramillo *et al.*, 2003a; Segura *et al.*, 2003). Instead, we found no differences in the C stocks among valleys and hills, at least for secondary forests. Moreover, C stocks in valleys were not related at all with forest age (Figure S4.2). It was difficult to find valley sites older than 20 yr, in this region, most probably because they are highly demanded for agricultural use. Because of this limitation, the ages of the valley sites in our sample spans mostly from 5 to 20 yr. Given the natural variation and the legacies of past use found in the Chamela-Cuixmala region, this sample could have not been enough to elucidate a pattern related to forest age. It is also likely that, given their location within a landscape of high agricultural use, secondary forests in valleys are more prone to be impacted by human activities like cattle grazing or timber extraction (Burgos y Maass, 2004), therefore constantly reducing C stocks and obscuring patterns related to forest age. The lack of difference in C stocks among hills and valleys seems therefore to reflect a sampling limitation or an increased use of these secondary forests.

Another expected but absent effect was that of present forest use, both in old-growth and secondary forests. Sites were selected to ensure that the three main types of use in the region (timber extraction, cattle browsing, stakes extraction) were included in our sample. However, no effect of the type or intensity of such uses was detected. Of course, this does not mean that C stocks or diversity are not reduced by these activities (Rendón-Carmona *et al.*, 2009; Edwards *et al.*, 2011; Berenguer *et al.*, 2014), but rather that other sources of variation have a higher effect. Also, it is likely that the effect of such management is currently evident only in certain, small size tree categories (Chaturvedi *et al.*, 2012), while the long-term consequences are not yet detectable. In any case, further studies are required to test to what extent current forest management practices lead to forest degradation, as has been previously found in the Chamela-Cuixmala region (Rendón-Carmona *et al.*, 2009) and in other TDFs (Pereira *et al.*, 2003; Álvarez-Yépiz *et al.*, 2008).

C-diversity association is mediated by those factors affecting C stocks and species diversity

The C-diversity association across the landscape is mainly driven by forest age. The combined increase of both attributes is the result of forests having greater C stocks and species diversity as they get older. Moreover, the statistical association between them disappears when the effect of forest age is taken into account. Previous work testing C-

diversity associations in the context of REDD+ has been done mostly at global or national levels, largely including data from non-highly transformed ecosystems (UNEP-WCNC, 2008; Venter *et al.*, 2009; Strassburg *et al.*, 2010). To our knowledge, the present study is the first attempt to test the C-diversity association across a human-modified landscape and the factors that explain it. In contrast with a previous meta-analysis which concluded that species diversity and particularly species composition recover at lower rates than C stocks (Martin *et al.*, 2013), our results suggest that in the Chamela-Cuixmala region the recovery of species diversity is coupled with aboveground C stocks recovery. Late successional forests ca. 40 yr show an almost complete recovery of both species diversity and C stocks, highlighting the importance of successional forests across human dominated landscapes (Castillo-Campos *et al.*, 2008; Chazdon *et al.*, 2009b, 2011a). This of course may depend on the degree of landscape transformation, which seems to be relatively low across this region (Sánchez-Azofeifa *et al.*, 2009).

In addition to the main effect of forest age, site factors also modulate the C-diversity association. In general, forests in sites more intensively managed show both reduced C stocks and reduced diversity. Previous studies have pointed out that increased management intensity can have long-lasting effects on the recovery of C stocks or species diversity throughout the tropics (Uhl *et al.*, 1982; Molina Colón y Lugo, 2006; Lawrence *et al.*, 2007; Mascaro *et al.*, 2011; Williamson *et al.*, 2012), although meta-analysis are not conclusive (Marin-Spiotta *et al.*, 2008; Martin *et al.*, 2013). Within the Chamela-Cuixmala landscape, factors affecting the recovery of C stocks or diversity differ, with previous land use intensity affecting C stocks, while the type of disturbance and landscape configuration affects species diversity. Since such effects are uncorrelated, increased C stocks (under light use intensity) can be true even for low species richness associated, for example, to mechanized forest clearing. In contrast, increased species richness associated to slash-and-burn deforestation can be associated to relatively low or high C stocks.

Differential landscape management strategies may involve different C and diversity benefits, but not necessarily reduced deforestation rates

From our analysis, a trade-off between reducing C emissions from deforestation and maintaining species diversity at the landscape scale emerged from the deforestation simulations. Reduced C emissions can be attained if forests with low ABC_T stocks are transformed to pastures or croplands, like young or even intermediate secondary forests, instead of forests with the highest C density, like old growth forests. However, in the Chamela-Cuixmala region, such reduction came at the cost of losing species diversity.

Secondary forests represent an important reservoir of species, which includes mostly old growth forest species but also secondary forests specialists (Álvarez-Yépez *et al.*, 2008; Castillo-Campos *et al.*, 2008; Lebrija-Trejos *et al.*, 2010a; Chazdon *et al.*, 2011b). Some strict early-successional species in the region are *Acacia macracantha*, *Mimosa acantholoba*, *Mimosa arenosa* and *Zanthoxylum sp.* What our simulations imply is that a deforestation process highly concentrated on these type of forests would cause the reduction in the incidence of some of these species through the landscape, particularly those such as *M. acantholoba* or *Zanthoxylum sp.*, which are not widespread but rather locally abundant in some successional sites (Romero-Duque *et al.*, 2007). Accordingly, under an evenly distributed deforestation scenario such reduction in species richness was not so marked, because a greater amount of early secondary forest remained. These results should however be taken only as indicative, since our simulations do not consider the potential role of pastures for conserving species, particularly those strict early successional, which are commonly present and able to reproduce in active pastures.

Reducing emissions from deforestation occurred even in the absence of a reduction of deforestation rates. We found that at equal or even higher deforestation rates than those present during the baseline period (1970-2005), reductions in landscape C stocks (*i.e.*, C emissions from deforestation) may not surpass the limit defined from such reference level. This is so because during the baseline period, deforestation occurred in old growth forests, with some portion of those deforested lands converted into secondary forests by the end of the period (2005). Net C losses were therefore calculated from the loss of high C density forests, *i.e.*, old growth forests. However, during the subsequent period, deforestation can occur on both old growth forests and secondary forests (Helmer *et al.*, 2008; Asner *et al.*, 2009; Wright, 2010). Moreover, local people often prefer to clear secondary than old-growth forests because of the reduced time and energy input required to do it (Burgos y Maass, 2004; F. Mora, *unpublished*). Since secondary forests have lower carbon density, as our own results show, the reductions in landscape ABC_T stocks can be lower than those expected from the baseline scenario, even at the same deforestation rates.

Reduced emissions at the same deforestation rates could also be related to the depletion of aboveground C stocks in TSEF. Although naturally restricted to only 11 % of the landscape in the study region, TSEF had been almost completely cleared until 2005 (Sánchez-Azofeifa *et al.*, 2009), and because of their high C density (Jaramillo *et al.*, 2003a), this forest type most likely contributed significantly to past emissions. The reduced extension of TSEF today (Sánchez-Azofeifa *et al.*, 2009) is not enough to cause the same emission levels by their transformation to secondary forests (*pers. obs.*) with the

subsequent reduction in C stocks. However, these forests continue to play an important role for diversity conservation at the landscape level. The sharp reduction in species richness when going from actual C-diversity values (0 % deforestation) to a 25 % deforestation level is associated to the complete disappearance of this forest type, and therefore of those species restricted to this habitat, like *Coccoloba barbadensis*, *Cordia seleriana*, *Couepia polyandra* or *Lonchocarpus guatemalensis*. Such potential reduction highlight the relevance of protecting all TSEF remnants, even if secondary, a goal that is currently attained at least partially by the Chamela-Cuixmala Biosphere Reserve (Sánchez-Azofeifa *et al.*, 2009).

Alternatives for implementing REDD+ across this human modified landscape and the potential management activities related

The results from both the site level C-diversity analysis and the landscape level deforestation simulations can be integrated in order to provide some guidelines for REDD+ implementation across this human modified landscape. Since forest age is the main driver of the C-diversity association, here we present such guidelines for different forest types defined mainly on the basis of forest age.

Old forests. Forest in this category, which included both secondary forest (> 40 yr) and old growth forests (with no modern record of disturbance), maximize both C stocks and species diversity at the site level, and their loss through deforestation could cause the highest C reductions across the landscape. Therefore their targeting for REDD+ seems highly desirable, although the potential carbon and diversity benefits depends on their actual conservation figure, strongly associated to land tenure. Old forests in the region are of two kinds. Those located within the Chamela-Cuixmala Biosphere Reserve (CCBR) are essentially private lands owned by two institutions, namely the National Autonomous University of Mexico (UNAM) and the Cuixmala Ecological Foundation (Castillo *et al.*, 2005; Maass *et al.*, 2005), both of which hold political and economic power, and have assigned the land of the CCBR to strict biological conservation. Therefore, implementing REDD+ within the CCBR would represent no additional gain for C or biodiversity, since the actual risk of forest transformation is almost absent. Those lands under strict conservation are however required for the maintenance of the C stocks and diversity associated to particular, cover-reduced habitats like TSEF. Such habitats may not be protected even under REDD+ implementation, due to the high opportunity costs associated (Balderas Torres *et al.*, 2013).

The other old forests are located beyond the CCBR and the great majority are owned by local peasants. Large tracks of these forests have not yet been cleared (Sánchez-Azofeifa *et al.*, 2009), most probably because of their distance to urban settlements and lack of infrastructure (roads, electricity, water supply) which make them very low profitable for productive activities. Nevertheless, they have been subjected to different intensity levels of cattle ranching and timber extraction (Burgos y Maass, 2004; Rendón-Carmona *et al.*, 2009; Cohen, 2014). Also, old forest patches are conserved amidst otherwise transformed landscapes because of the owners' interest to keep them as a source of timber and additional fodder for cattle (Cohen, 2014). These forests would highly fit for REDD+ implementation. They not only maximize C stocks and diversity, but face a real risk of being deforested, particularly those located within transformed landscapes (Phelps *et al.*, 2012a). Management options under REDD+ could include C stocks conservation (Angelsen, 2008; Parrotta *et al.*, 2012), particularly for the large tracks of forest located far from human settlements. A similar conservation tool has been already implemented in some areas near the CCBR, under the scheme of payment for biodiversity conservation (<http://www.conafor.gob.mx/portal/index.php/pronafor>). A sustainable forest management could also be implemented, particularly in old forest patches located within heavily modified landscapes, which are more susceptible to be transformed (Helmer *et al.*, 2008). Although we found no evidence of C stocks degradation in old forests managed for cattle ranching or timber extraction, the long-term effects of those activities may not be evident yet (Chaturvedi *et al.*, 2012). Sustainable management activities could reduce future C emissions without compromising the provision of benefits local owners obtain from them.

Intermediate forests. "Second Tier" sites for REDD+ would be secondary forest in an advanced regeneration stage (18 to 40 yr). Although their conservation would bring out slightly smaller diversity benefits in comparison to old forests, their C benefits would be high because of their higher deforestation probability (Helmer *et al.*, 2008). These forests also have the potential for additional C sequestration (Mora *et al.* *submitted*), and therefore their disappearance would imply a "C opportunity cost", *i.e.*, future gains of C would be lost. These benefits are potentially higher in intermediate secondary forest growing on lands subjected to light use.

The implementation of REDD+ can, however, become struggling in intermediate forests because of the possible trade-offs between actual land uses and potential future benefits. Implementing REDD+ in both old and intermediate forests would imply either a deforestation displacement towards young forests, or an overall reduction in deforestation rates across the landscape. Displacement to young forests could imply a net reduction in

landscape diversity as suggested before, while reduction in deforestation rates may imply an increase in management intensity of the already available croplands and pastures (Miles y Kapos, 2008), or a net reduction in such productive activities, which in principle should be offset by the economic benefits caused by REDD+ (Miles y Kapos, 2008; Phelps *et al.*, 2012a). Between the two scenarios, probably a total translocation of deforestation towards young secondary forests would be a better solution, since the loss of diversity may be dominated by secondary forest specialists. However, since an increased intensity of use could lead to drastic reductions in their productive capability on the long term (Lawrence *et al.*, 2007) or in their capacity to provide other ecosystem services (Trilleras *et al.*, 2015), sustainable management practices of those cleared lands are required.

Young forests. The “last Tier” of sites for the implementation of REDD+ across this human modified landscape would be young secondary forests (< 18 yr). They hold both low C stocks and diversity, and therefore the benefits of including them in REDD+ would be very low (Phelps *et al.*, 2012a). However, if their carbon capture potential is taken into account, those sites should be of high priority. Among all the forest types present in the region, young secondary forests tend to accumulate C faster (Mora *et al.* *submitted*). Their deforestation would then imply a “high C opportunity cost”. At the landscape level, this capture potential is relevant if there is no deforestation leakage into other areas, and therefore implies a net reduction in deforestation rates.

Active management activities, such as forest restoration, could be adopted for young forests sites to be of higher interest for implementing REDD+. Forest restoration activities that enhance C stocks or biodiversity beyond a baseline C accumulation scenario expected for such re-growing forests could provide additional benefits for C and diversity (Pichancourt *et al.*, 2014). Some of these sites, particularly those existing within landscapes with high proportion of croplands, seem to be best suited for such activities, due to their reduced species diversity. Moreover, some of these sites may be ongoing a sort delayed succession, associated to the dominance of only a few species, such as *Mimosa acantholoba* or *Mimosa arenosa*, forming a thorny vegetation. Although in the forest understory of such sites a seedling community similar to that of more advanced successional stages can be establishing (Romero-Duque *et al.*, 2007), active management of those sites through enrichment planting with species of high C accumulation or that retain more C on the long term (Mora *et al.* *submitted*; Pichancourt *et al.*, 2014, but see Ruiz-Jaen y Potvin, 2011), or through selective cutting that favors tree establishment and growth, could be implemented.

Conclusions

The REDD+ scheme is probably one of the most widely discussed climate change mitigation strategies because of its C benefits, but also because of its potential implications (positive or negative) on other aspects of forest management, like biodiversity or community rights on forests. Safeguarding such aspects is a prerequisite for its adequate implementation. In this work we have shown that by assessing the implications of both biophysical conditions and land use history on carbon stocks and biodiversity, a better picture on where to implement REDD can be accomplished. From this analysis, secondary forest, now widely distributed within transformed tropical landscapes, could also be selected for REDD implementation because of their high diversity value and their relatively high or even increasing C stocks. Furthermore, we have shown that, at a regional level, several routes to reducing emissions from deforestation exists if we account for the presence of secondary forests, each of which have different implications in terms of C emissions and biodiversity conservation. This kind of analysis could therefore serve as a tool for taking decisions on where to implement REDD+.

Aknowledgements

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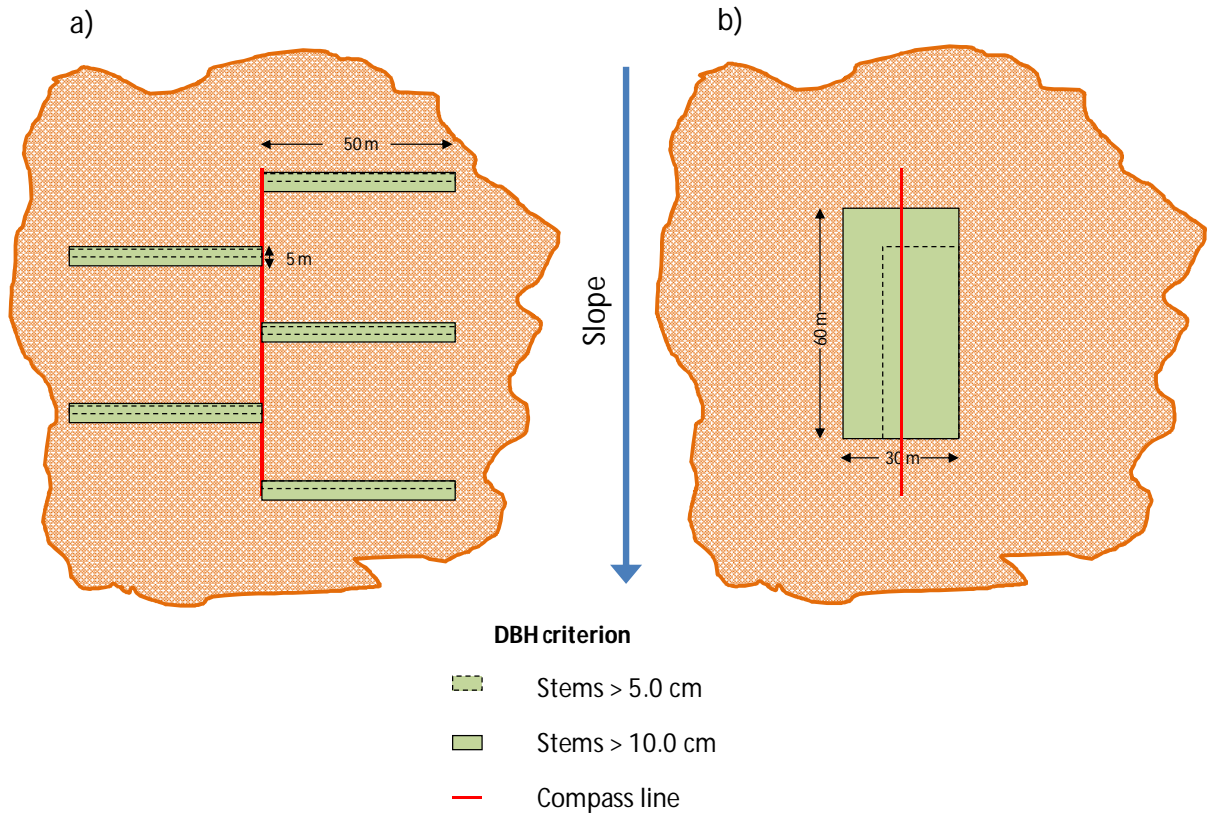


Figure S4.1. Sampling designs used in this study. a) Thirty eight sites were sampled using a Gentry-like protocol modified from Baraloto *et al.* (2013). b) Twelve sites were sampled using a previously established plots for the long-term study of forest dynamics in secondary and old-growth forests (Martínez-Ramos *et al.*, 2012). Red lines indicate the major axis of each site, running downslope on sites located on hills or to the north in sites on valleys.

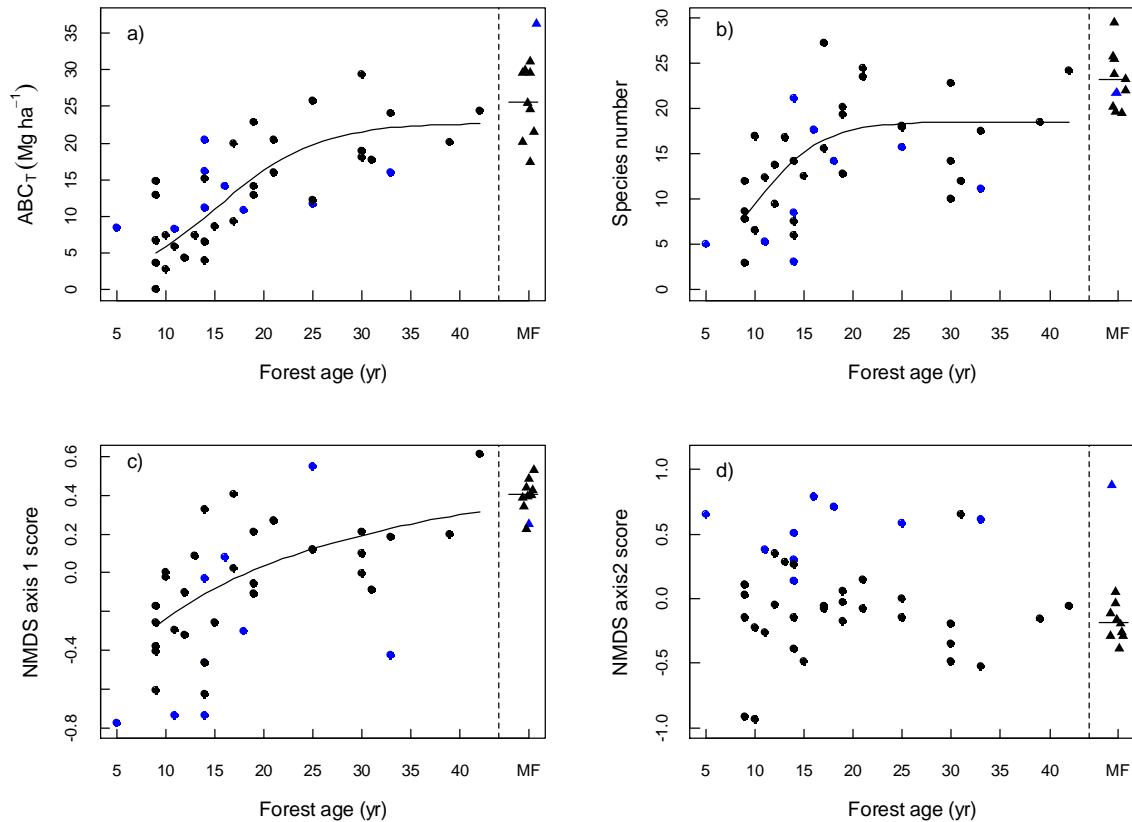


Figure S4.3. Change in forest attributes in relation to forest age. a) Carbon stock in aboveground living biomass of trees (ABC_T), b) Carbon based rarefied richness, c) and d) Species composition, measured through the first two axes of a non-metric multidimensional scaling ordination (NMDS). Black color represents sites on hills, while blue color denotes sites on valleys. Continuous lines represent models fitted depicting a significant statistical relationship between variables. Note that no significant relationship was found for valleys. Old-growth forests (triangles) are shown as reference but were not included for model fitting. OGF = Old-growth forests

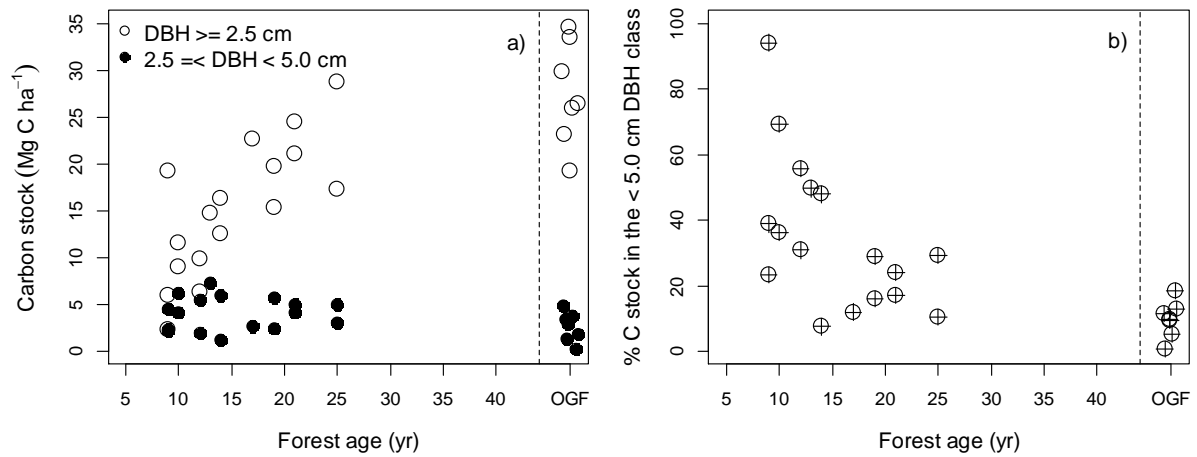


Figure S4.2. Contribution of stems 2.5-5.0 cm DBH to forests aboveground living biomass C in trees (ABC_T) in relation to forest age. a) ABC_T in all the stems (≥ 2.5 cm DBH) and the smallest DBH category ($2.5 \leq DBH < 5.0$ cm), b) relative contribution of the smallest stems to the total ABC_T . OGF = Old growth forests.

Table S4.1. Site variables used to characterize forest age, topography, previous land use and landscape configuration in the Chamela-Cuixmala region. References are provided for studies on the effect of those variables on carbon stocks or species diversity in tropical regions.

Variable type	Variable name	Description	Value range or units	References
Forest age	Forest age	Length of period of forest regrowth. Calculated from the last year of at least one of the common intentional management activities used to remove vegetation (cultivation, slashing, burning, or herbicide application)	Years, old-growth forests included as 100 yr	(Becknell <i>et al.</i> , 2012; Martin <i>et al.</i> , 2013)
Topography	Topographic position	Site location relative to topographic variation	Hill, valley	(Jaramillo <i>et al.</i> , 2003a)
	Slope Google Earth	Mean terrain slope (vertical change in relation to the horizontal displacement) measured along the main site axis using the Google Earth elevation profile option	Unitless	
	Slope GPS	Mean terrain slope (vertical change in relation to the displacement on the terrain surface) measured along the main site axis. Elevation values taken with a GPS device along the main site axis	Unitless	
	Mean elevation	Mean elevation above sea level derived from five elevation measurements taken along the main site axis at regular distances	meters	
	Aspect	Cosine of the slope direction	Unitless	(Balvanera <i>et al.</i> , 2002)
Previous land use	Timber extraction	Presence of timber extraction activities in old-growth forests or during forests regrowth in secondary forests	Yes/No	(Berenguer <i>et al.</i> , 2014)

Timber intensity	extraction	An ordinal scale to assess the intensity of timber extraction	0 (no extraction), 1 (light extraction reported, < 10 trees ha ⁻¹ , with equivocal evidence of extraction in the field [stumps absent]), 2 (heavy extraction reported, >10 trees/ha, with clear evidence of extraction in the field [stumps present])	
Understory slashing		Evidence of understory slashing, including stake extraction and understory clearing for cattle browsing	Yes/No	(Rendón-Carmona <i>et al.</i> , 2009)
Understory intensity	slashing	An ordinal scale to assess the intensity of selective understory slashing	0 (no slashing), 1 (light or selective slashing reported by land owner but with equivocal evidence in the field), 2 (heavy, selective [stake extraction >200 stakes/ha] or non-selective [understory clearance] slashing, with clear evidence in the field [presence of stumps]).	
Cattle presence		Presence of cattle in the forest	Yes/No	(Chaturvedi <i>et al.</i> , 2012)

Cattle ranching intensity	An ordinal scale to assess the intensity of cattle ranching in the forest understory	0 (no cattle present), 1 (sporadic, very low density cattle, < 10 head ha ⁻¹ during at least one month, no cattle feces or paths seen), 2 (frequent, intermediate cattle density, >10 heads ha ⁻¹ during at least one month, sporadic feces and no or < 2 cattle walks seen within the site), 3 (frequent, very high cattle density, >10 heads ha ⁻¹ in at least one month, along with high density of feces and cattle paths)	
Understory use index 1	The maximum value between timber extraction intensity, understory slashing intensity, and cattle ranching intensity	0 to 3	
Understory use index 2	The sum of the values of timber extraction intensity, understory slashing intensity, and cattle ranching intensity	0 to 7	
Forest clearance	Known previous forest clearance	Yes/No	(Gibson <i>et al.</i> , 2011; Berenguer <i>et al.</i> , 2014)
Forest clearing type	When present, the kind of forest clearance implemented	None, Slash-and- burn, Bulldozer	
Age of forest clearance	Time since the site was first cleared	Years (not applicable to non-cleared sites)	
Main use	Main use between forest clearance and the beginning of forest regrowth	None (cleared but not used), agriculture, pasture for cattle ranching, or not applicable (when no previously cleared)	(Molina Colón y Lugo, 2006)

	Additional use	Secondary use between forest clearance and the beginning of forest regrowth	None (cleared but not used), agriculture, pasture for cattle ranching, or not applicable (when no previously cleared)	
	Maintenance activities	The kind of maintenance activities for the continued use of the site between forest clearance and the beginning of forest regrowth. Can include more than one activity.	Repeated cultivation (in agricultural lands), slashing, burning, herbicide application, none, or not applicable (when no previously cleared)	
	Maintenance frequency	Times the maintenance was done before forest regrowth	0 to 20, or not applicable (when no previously cleared)	
	Duration of use before forest regrowth	Length of time the elapsed between first forest clearance and the last application of at least one of the maintenance activities	Years (not applicable to non-cleared sites)	(Orihuela-Belmonte <i>et al.</i> , 2013)
	Duration of temporary abandonment	Maximum length of time the site was left without use previous to final forest regrowth	Years (not applicable to non-cleared sites)	
Landscape configuration	Forest cover	Percentage of forest cover within a 1-km radius around the midpoint of each site, evaluated for the last available Google Earth satellite image (2013-2014)	%	(Jakovac <i>et al.</i> , 2015)
	Early successional forest cover	Percentage of forest cover < 9-10 yr old within a 1 km radius around the midpoint of each site. Evaluated by comparison of the oldest and last available Google Earth satellite images (2003-2004 to 2013-2014)	%	

Non-early successional forest cover	Percentage of forest cover > 10 yr old within a 1-km radius around the midpoint of each site. Evaluated by comparison of the oldest and last available Google Earth satellite images (2003-2004 to 2013-2014)	%
Agriculture land	Percentage of agricultural lands within a 1-km radius around the midpoint of each site. Evaluated by comparison of the oldest and last available Google Earth satellite images (2003-2004 to 2013-2014)	%
Pasture land	Percentage of pasture lands within a 1-km radius around the midpoint of each site. Evaluated by comparison of the oldest and last available Google Earth satellite images (2003-2004 to 2013-2014)	%

Capítulo 5. *Discusión general*

Francisco Mora

El estudio de la sucesión secundaria en campos agropecuarios abandonados de las regiones tropicales secas ha sido un área de investigación científica de rápido crecimiento en el campo de la ecología durante la última década. A la fecha existen ya numerosos trabajos que documentan los patrones generales de cambio de múltiples atributos del bosque tropical seco (BTS) a través de la sucesión, particularmente para el continente americano (Uhl *et al.*, 1982; Kalacska *et al.*, 2004; Ruiz *et al.*, 2005; Vargas *et al.*, 2008; Madeira *et al.*, 2009; Hernández-Stefanoni *et al.*, 2010; Lebrija-Trejos *et al.*, 2010a, 2010b; Maza-Villalobos *et al.*, 2011; Becknell *et al.*, 2012; Dupuy *et al.*, 2012; Lohbeck *et al.*, 2013; Pineda-García *et al.*, 2013). Sin embargo, la recuperación de las funciones del bosque y de los beneficios que de éstas se derivan es aún un área de estudio relativamente poco explorada (Sánchez-Azofeifa *et al.*, 2005; Kauffman *et al.*, 2009; Quesada *et al.*, 2009). En el contexto actual del cambio global, entender el papel que juega la transformación de las áreas tropicales en el ciclo del carbono y en la conservación de la biodiversidad constituye todavía un reto para la ciencia, con implicaciones importantes para la mitigación del cambio climático y para la generación de estrategias de manejo de las áreas tropicales que incrementen los beneficios tanto para los pobladores locales como para las sociedades en general (Chazdon *et al.*, 2009a; Chazdon, 2014).

El objetivo central de esta tesis fue el de generar información científica acerca de la variación espacial y temporal de los almacenes de C asociados al BTS en la región de Chamela-Cuixmala, mediante la evaluación de los factores que afectan la recuperación de la estructura, la diversidad y los almacenes de carbono durante de la sucesión secundaria en campos agropecuarios abandonados en un paisaje de BTS. Este análisis fue motivado por la posibilidad de proveer elementos de juicio y herramientas prácticas de apoyo para la toma de decisiones relacionadas con el manejo del BTS en general y para la aplicación de esquemas de manejo del C almacenado en estos bosques en particular. En este capítulo presento una discusión general en torno a esas dos metas planteadas al inicio del estudio, es decir, sobre el avance en el conocimiento científico aportado por este trabajo y sobre sus implicaciones para el manejo del BTS.

La integración de aproximaciones de cronosecuencia y dinámica para el estudio de la sucesión secundaria

La gran mayoría del conocimiento con el que contamos actualmente sobre la sucesión secundaria en las regiones tropicales ha sido generado a través del uso de cronosecuencias; es decir, mediante la caracterización de una secuencia de sitios en distintas etapas de la sucesión. Sólo hasta hace pocos años se comenzaron a explorar aproximaciones

complementarias o alternativas, tales como el análisis de anillos de crecimiento de los árboles (Brienen *et al.*, 2009), la percepción remota, ya sea por medio de imágenes de satélite de alta resolución o de imágenes de radar (Gallardo-Cruz *et al.*, 2012; Martinuzzi *et al.*, 2013), o bien mediante el monitoreo permanente de las áreas en sucesión a través del tiempo (Chazdon *et al.*, 2007; Van Breugel *et al.*, 2007; Lebrija-Trejos *et al.*, 2010a; Maza-Villalobos *et al.*, 2011). El seguimiento a través del tiempo (aproximación dinámica) ha permitido evidenciar que si bien la dinámica sucesional de los bosques secundarios puede seguir el patrón general definido por la cronosecuencia, es también muy común su desviación (Chazdon *et al.*, 2007; Norden *et al.*, 2015). Una de las aportaciones más relevantes del presente trabajo es el haber comprobado la discrepancia existente entre la recuperación sucesional que se puede proyectar a partir de las cronosecuencias y la dinámica de corto plazo de los bosques sucesionales, a través de la implementación de una aproximación estadística que permitió poner a prueba las proyecciones de la cronosecuencia (Capítulos 2 y 3). Más aún, el uso de dicha aproximación sugiere que, en contra de lo esperado, la recuperación de los atributos estructurales y el almacén de carbono aéreo durante la sucesión son mucho menos predecibles en el corto plazo que la diversidad de la comunidad de árboles.

Derivado de este análisis y de trabajos previos sobre la discrepancia entre las aproximaciones de cronosecuencia y dinámica, vale la pena cuestionarse cuál es el valor de las cronosecuencias para el estudio de la sucesión secundaria. Por supuesto, ésta no es la primera vez que se plantea dicha pregunta (Johnson y Miyanishi, 2008; Walker *et al.*, 2010), pero esta tesis ofrece nuevos elementos que aportan a la discusión. En el Capítulo 2 se demostró que aun en el caso de una cronosecuencia establecida en sitios con condiciones físicas similares, fue posible detectar efectos de diferencias no advertidas previamente en su historia de manejo, o de la configuración del paisaje, sobre la recuperación de los atributos del bosque. La diversidad de estrategias de manejo en la región de Chamela-Cuixmala y el amplio abanico de actividades asociadas (Burgos y Maass, 2004; Cohen, 2014; Trilleras *et al.*, 2015), así como su aparente cambio a través del tiempo, hacen casi imposible asegurar la homogeneidad de condiciones para la cronosecuencia (Quesada *et al.*, 2009). A pesar de ello, la ausencia de condiciones similares, más que una debilidad de la aproximación de cronosecuencia, representa una oportunidad para el estudio de los factores que determinan la sucesión secundaria en el BTS, por ejemplo, a través de la comparación de los patrones sucesionales resultantes de cronosecuencias establecidas en condiciones biofísicas o de manejo contrastantes (Uhl *et al.*, 1982, 1988; Powers *et al.*, 2009; Mwampamba y Schwartz, 2011; Becknell *et al.*, 2012). De manera alternativa, es posible documentar de manera detallada para cada sitio incluido en la cronosecuencia las

condiciones biofísicas en las que se encuentra, así como su historia de manejo, para luego poner a prueba su efecto sobre la sucesión (Dupuy *et al.*, 2012). Ésta fue la aproximación que empleé en el presente trabajo (Capítulos 2 y 4). Obtener evidencia de este tipo de efectos a través del uso de aproximaciones dinámicas es inviable, tanto por la escala temporal a la que opera el fenómeno de la sucesión, como por la posibilidad real de desarrollar tal tipo de experimentos (Walker *et al.*, 2010).

Los resultados obtenidos en la presente tesis doctoral indican la necesidad y la pertinencia de combinar diferentes aproximaciones para el estudio de la sucesión secundaria en campos tropicales abandonados. Por una parte, las cronosecuencias ofrecen un escenario adecuado para poner a prueba de hipótesis acerca de mecanismos y procesos sucesionales que ocurren en escalas de décadas o siglos, mientras que los estudios dinámicos permiten obtener detalles acerca de los cambios en el corto plazo, cómo éstos varían sujetos a condiciones que se presentan a escalas de tiempo menores (p.ej. fluctuaciones en las condiciones climáticas entre años) o permiten la cuantificación directa de las funciones del ecosistema, entre las que se encuentran la acumulación de carbono en la biomasa. Los resultados también confirman la necesidad de tomar en cuenta estas limitantes a la hora de estimar y predecir, con base en las cronosecuencias, los cambios que en el corto plazo puedan tener los atributos y funciones del bosque en distintas etapas de la sucesión.

Sucesión secundaria en la región de Chamela-Cuixmala en el contexto de los bosques tropicales secos

El BTS ha sido considerado como un ecosistema altamente resiliente, debido a su aparentemente acelerada recuperación luego de disturbios de diferente naturaleza (Murphy y Lugo, 1986). Sin embargo, no existe a la fecha una prueba inequívoca de que la recuperación del BTS sea particularmente rápida (Lebrija-Trejos *et al.*, 2008; Martin *et al.*, 2013). La evidencia presentada en este trabajo sugiere que, al menos en el caso de la sucesión secundaria en la región de Chamela-Cuixmala, dicha resiliencia depende de manera importante del tipo de atributo que se seleccione para medirla. La recuperación de los atributos estructurales y de la diversidad (riqueza y composición) de la comunidad de árboles se da de manera relativamente rápida, de tal forma que bosques con edades superiores a los 18 años son muy similares a los bosques maduros (Capítulos 2 y 4). La rápida recuperación de la composición de especies en la región es particularmente notoria, si se le compara con la observada en otras regiones tropicales, lo cual ha llevado a cuestionar la posibilidad de que los bosques secundarios actúen como reservorios de la

biodiversidad en los paisajes transformados (Gibson *et al.*, 2011; Martin *et al.*, 2013; van Breugel *et al.*, 2013). Por el contrario, la recuperación de los almacenes de C no es tan acelerada. Los almacenes aéreos muestran una recuperación un poco más lenta que la de los atributos estructurales, de tal forma que sólo después de 30 años de abandono llegan a presentar valores dentro del intervalo observado para los bosques maduros (Capítulos 3 y 4). Dicha velocidad de recuperación parece estar en el intervalo de valores reportados previamente para otros BTS del mundo (Vargas *et al.*, 2008; Becknell *et al.*, 2012; Martin *et al.*, 2013). En cambio, los almacenes de C subterráneos y particularmente los de mayor tamaño (biomasa de raíces gruesas y C orgánico en el suelo) no presentan una tendencia a la recuperación, al menos durante los primeros 20 años de crecimiento del bosque (Capítulo 3). Si bien en conjunto estos resultados indican que el bosque recupera buena parte de sus características en un período de tiempo relativamente corto (aproximadamente 30 años), la recuperación del ecosistema en su totalidad y particularmente de los almacenes de C es seguramente un proceso que ocurre a la escala de varias décadas, como se ha observado en otras regiones tropicales (Mascaro *et al.*, 2011; Marin-Spiotta y Sharma, 2013).

Otro aporte importante de la presente investigación es que demuestra la importancia de las condiciones del sitio, particularmente de la historia de manejo, para la recuperación del bosque a través de la sucesión secundaria. La recuperación de los atributos estructurales, pero sobre todo de la diversidad y de los almacenes aéreos de C, se encuentra negativamente influenciada por la intensidad del manejo previo (Capítulos 2 y 4). El efecto negativo del incremento en la intensidad de manejo sobre la recuperación a través de la sucesión ha sido ampliamente documentado (Chazdon, 2008; Eaton y Lawrence, 2009; Orihuela-Belmonte *et al.*, 2013; Jakovac *et al.*, 2015). La novedad de los resultados obtenidos en el presente estudio radica en entender que tales efectos no se presentan necesariamente de manera uniforme a través de la cronosecuencia, sino que son evidentes en sitios pertenecientes a categorías de edad particular. Más aún, diferentes características del manejo tienen impactos sobre diferentes atributos del bosque. La complejidad de los efectos de la historia de manejo está relacionada con la alta idiosincrasia asociada a la dinámica sucesional y por ende a su baja predictibilidad (Norden *et al.*, 2015). Los resultados de esta investigación sugieren además la necesidad de diseñar estrategias de manejo del BTS que no impliquen necesariamente un incremento en la intensidad de uso, lo cual podría poner en riesgo la resiliencia del BTS en el futuro (Lawrence *et al.*, 2007; Trilleras *et al.*, 2015).

Estimación de los almacenes de carbono en los bosques secundarios secos de la región de Chamela-Cuixmala

El presente estudio constituye uno de los pocos esfuerzos que han hecho para estimar los almacenes de C al nivel ecosistémico en el BTS secundario. Varios resultados poseen implicaciones importantes para la estimación de los almacenes de C en este tipo de sistemas y de su papel en los flujos de C en la región tropical. Existen muy pocas estimaciones directas del almacén de C en raíces para el BTS (Jaramillo *et al.*, 2003a; Romero-Duque, 2008; Vargas *et al.*, 2008), de tal forma que la mayoría de las estimaciones se han realizado mediante el empleo de ecuaciones alométricas que relacionan la biomasa aérea con la subterránea (Mokany *et al.*, 2006). Sin embargo, la ausencia de una relación entre el almacén de C en las raíces gruesas y la edad sucesional o con el almacén aéreo implica que dicha generalización no es aplicable en el caso de los bosques secundarios de la región de Chamela-Cuixmala. Nuestros resultados sugieren también que las tasas de acumulación de C en la biomasa aérea del BTS secundario reportadas previamente y que son empleadas para estimar la contribución de los bosques tropicales al ciclo global del C (IPCC, 2006; Bonner *et al.*, 2013; Grace *et al.*, 2014) podrían constituir sobrestimaciones importantes de las tasas de acumulación real (Capítulo 3). Éstas han sido derivadas en su mayoría de estudios de cronosecuencia, que, como se discutió previamente, no permiten generar predicciones precisas de los cambios reales en el tiempo. La cuantificación del papel de los bosques secundarios en contribuir o mitigar el cambio climático depende de manera importante de dichas estimaciones (Houghton, 2003; Wright, 2010; Pan *et al.*, 2011), por lo que se requieren estudios adicionales de este tipo, en una extensión mayor de BTS a nivel de distintas regiones del mundo, que aborden este tema.

La diversidad biológica: tanto una necesidad como un beneficio

Una de las dimensiones más importantes del cambio global es la pérdida de la diversidad biológica y con ello, la reducción de la capacidad de los ecosistemas de desempeñar sus funciones y por ende, de proporcionar los beneficios que de ellos obtenemos (Díaz *et al.*, 2006; Cardinale *et al.*, 2012; Lefcheck *et al.*, 2015). En particular, tanto la productividad como el almacenamiento de C en los bosques tropicales están relacionados con diferentes aspectos de la diversidad de la comunidad de árboles (Chisholm *et al.*, 2013; Finegan *et al.*, 2015). Sin embargo, la evidencia del efecto de la acumulación de especies propia de la sucesión sobre la recuperación de las funciones ecosistémicas es reducida (Conti y Díaz, 2013; Lasky *et al.*, 2014). Más aún, cualquier asociación entre diversidad y función en un contexto sucesional puede ser simplemente resultado del efecto

del paso del tiempo actuando como una causa común sobre la diversidad y la función, más que evidencia inequívoca del papel funcional de la diversidad. Por ejemplo, Lohbeck *et al.*, (2015b) encontraron que la diversidad tiene un papel modesto en la acumulación de C a través de la sucesión secundaria del bosque tropical húmedo, a pesar de los cambios observados en diversidad asociados a dicho proceso.

En este trabajo encontré que para el caso del BTS de la región Chamela-Cuixmala, indicadores de diversidad de especies y atributos funcionales particulares se encuentran asociados tanto a los almacenes de C como a su cambio a través del tiempo (Capítulo 3). Sin embargo, la altura máxima de las especies (un rasgo funcional que indica el tamaño de cada especie) fue la única variable asociada positiva y consistentemente con los almacenes de C y sus tasas de cambio. Esta asociación constituye una evidencia del papel funcional de la diversidad, puesto que no es explicada por la edad del bosque o la biomasa de la comunidad vegetal. Sin embargo, el efecto del tamaño de las especies sobre la tasa de acumulación de C no es consistente a través del tiempo, sino que posiblemente se incrementa en condiciones biofísicas extremas (en particular, de disponibilidad de agua). Los resultados confirman entonces que la diversidad funcional tiene una relación causal con la acumulación de C, medida directamente (a través de datos dinámicos) o indirectamente a través de los almacenes de carbono de los bosques secundarios.

Si la diversidad biológica tiene un papel funcional durante la sucesión, el diseño e implementación de esquemas de conservación, manejo e incremento de los almacenes de C debe incluir a la conservación de la diversidad biológica como un requisito (Díaz *et al.*, 2009). En este trabajo encontré una asociación espacial importante entre la diversidad de especies y el tamaño del almacén de C en la biomasa aérea (Capítulo 4). Dicha asociación implica que la implementación de esquemas de pago por servicios ambientales del programa REDD+ puede traer como beneficio adicional, de manera relativamente sencilla, la conservación de la diversidad (Venter *et al.*, 2009; Phelps *et al.*, 2012a). Más aún, la implementación de REDD+ puede permitir la protección no sólo de los bosques maduros, en los que se maximizan tanto los almacenes de C como la diversidad, sino también de los bosques secundarios, principalmente los de mayor edad, en los que tanto los almacenes de C como la diversidad están cerca de sus potenciales máximos, al mismo tiempo que guardan aún cierta capacidad de acumulación neta de carbono (Capítulo 3). Este resultado sugiere también que la implementación de REDD+ mediante la inclusión de bosques secundarios no sólo retribuiría sobre la conservación o el incremento de los almacenes de C, sino también sobre la posibilidad de mantener otro tipo de beneficios directos para la población derivados de estos bosques (Cohen, 2014).

Los bosques tropicales secos en el contexto del cambio global

Aunque existe en la actualidad una buena cantidad de información acumulada sobre la recuperación de los BTS a través de la sucesión, la información en torno a la recuperación de los almacenes de C es aún escasa, en parte porque estos bosques han sido identificados como menos importantes que su contraparte húmeda (*i.e.*, bosques tropicales lluviosos o perennifolios), tanto como fuentes de gases de efecto invernadero, como sumideros de C. A pesar de ello, la conservación de los almacenes de carbono asociados al bosque tropical seco es relevante dada su extensión espacial (generan la tercera parte de las emisiones tropicales por deforestación, ver Achard *et al.*, 2014) y la alta diversidad biológica que albergan a escala global (Miles *et al.*, 2006; Pennington *et al.*, 2009). Además, la estimación adecuada de sus almacenes de C permite reducir la incertidumbre en torno a la contribución real de las áreas tropicales en el escenario de cambio climático global.

En el presente estudio se abordaron varios aspectos de la recuperación de los almacenes de C a través de la sucesión en el BTS y su conservación en un paisaje transformado por actividades humanas. Los resultados obtenidos indican que si bien la magnitud de los almacenes de C en este paisaje no es muy grande si se le compara con otras regiones tropicales, la conservación de dichos almacenes puede ayudar a mitigar tanto el cambio climático, a través de la reducción de las emisiones de gases de efecto invernadero, como la alta diversidad biológica contenida en esta región en particular. Más aún, este estudio indica que en el paisaje actual de la región de Chamela-Cuixmala, los bosques presentan una resiliencia relativamente alta y que, debido a la asociación tanto funcional como espacial entre la diversidad y los almacenes de C, la conservación e incremento de los almacenes de C puede constituir una estrategia potencial para la conservación y manejo de este ecosistema en el largo plazo.

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Anexo 1. *Sobretiro del artículo requisito*

Testing Chronosequences through Dynamic Approaches: Time and Site Effects on Tropical Dry Forest Succession

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ABSTRACT

Chronosequences, commonly used to assess succession, have been questioned because of their failure to project successional trajectories. Here, we develop a simple analytical approach combining both chronosequence and dynamic data to test the power of age of abandonment and site factors to explain and predict succession. The approach proceeds by first fitting statistical models relating age to attribute values (the chronosequence model) and their observed changes (the dynamic model) to test explanatory power. Predictive power is then tested by bootstrapping the chronosequence model to derive confidence intervals for expected changes and comparing them with the dynamic model. Finally, residuals from both models are tested against site factors. The procedure was applied to six attributes (basal area, plant density, mean plant height, species richness, evenness, and composition) of the woody community (plants >1 cm dbh within 0.1-ha plots) in nine abandoned cattle pastures (0–12 yr) and three old growth tropical dry forests monitored over 6 yr. Age explained 60–97 percent of the variance in community attributes and only 32–57 percent in observed changes. It significantly overestimated basal area and mean height, while species richness and composition were highly predicted. Besides age, management history also explained successional dynamics. Our results suggest age is not necessarily a reliable predictor of short-term successional dynamics, and explanatory power is not indicative of predictive power. Because of this low reliability, caution is needed when applying chronosequences to evaluate ecosystem services' recovery. The analytical approach developed here contributes to a better exploration of those possible limitations.

Abstract in Spanish is available in the online version of this article.

Key words: Chamela; land use history; Mexico; nonlinear models; rates of change; soil conditions; successional trajectories; surrounding matrix.

SECONDARY FORESTS WILL LIKELY DOMINATE FUTURE TROPICAL LANDSCAPES. Old growth tropical forests have been transformed mainly for the expansion of agriculture (Geist & Lambin 2002, Sanchez-Azofeifa & Portillo-Quintero 2011), but agricultural fields are often abandoned because of productivity loss or change in socio-economic context (Wright 2005). Secondary forests developing in these abandoned fields are becoming increasingly representative of tropical landscapes, reclaiming up to one-third of the original deforested area (Wright 2005, Foley *et al.* 2007). Understanding how these forests change in the course of succession is critical for ensuring biodiversity conservation and maintaining the supply of ecosystem services in tropical regions (Barlow *et al.* 2007, Chazdon *et al.* 2009).

Research on secondary succession in abandoned agricultural fields has mostly relied on the use of the chronosequence approach, where successional change is inferred by relating the time since field abandonment to plant community attributes such as basal area, biomass or species richness (Pickett 1989, Walker *et al.* 2010). The chronosequence approach, however, has been

challenged (Johnson & Miyanishi 2008). First, there is large variation in the explanatory power of age of abandonment, associated with differences in previous use or environmental conditions among sites (Marin-Spiotta *et al.* 2008, Mwampamba & Schwartz 2011, Dupuy *et al.* 2012), or with the community attribute being analyzed (Chazdon 2008, Lebrija-Trejos *et al.* 2008, Muñiz-Castro *et al.* 2011). Second, there is an apparent inability to project successional trajectories, since changes over time in ecosystem attributes do not necessarily match successional trajectories or rates of change inferred from chronosequences (van Breugel *et al.* 2006, Chazdon *et al.* 2007, Feldpausch *et al.* 2007, Maza-Villalobos *et al.* 2011, but see Foster & Tilman 2000). These challenges raise questions about the particular situations and variables for which chronosequences would adequately describe successional change (Walker *et al.* 2010) and, therefore, about its applicability to project the recovery of ecosystem attributes such as biomass and carbon stocks (Feldpausch *et al.* 2007, Johnson & Miyanishi 2008).

An improved understanding of succession could be achieved if chronosequences were complemented with a dynamic approach by monitoring sites through time. This would allow for a test of the match between successional trajectories projected from chro-

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nosequences and those derived from repeated measurements (Pickett 1989, Foster & Tilman 2000, Chazdon *et al.* 2007). However, there are relatively few dynamic studies of tropical succession (Chazdon *et al.* 2007, Lebrija-Trejos *et al.* 2010, Williamson *et al.* 2012). In addition, there is a lack of adequate, statistically based tests for chronosequence-based inferences (Feldpausch *et al.* 2007, Johnson & Miyanishi 2008). Tests have mostly relied on the visual comparison of the trajectories from chronosequence and dynamic observations or on correlations between age of abandonment and observed community changes (Foster & Tilman 2000, Chazdon *et al.* 2007, Maza-Villalobos *et al.* 2011, Williamson *et al.* 2012). These approaches do not test for specific trajectories or rates of change expected from chronosequence models.

The effect of site factors should also be taken into account to improve our understanding of succession. There is extensive evidence suggesting that factors like field management history, soil properties, and adjacent forest cover can influence succession (Holl 1999, Guariguata & Ostertag 2001, Chazdon 2003, 2008). Their effects may depend upon the attribute analyzed. Species diversity and composition are expected to be dependent primarily on both the presence of remnant vegetation, and on the properties of the forest matrix around sites (Purata 1986, Holl 1999, Norden *et al.* 2009). On the other hand, structural attributes have shown to be highly influenced by previous land use, particularly the type of land clearance or the frequency of fires (Uhl *et al.* 1988, Moran *et al.* 2000), although they can also influence species composition (Mesquita *et al.* 2001). Most of the chronosequence studies, however, rely on the assumption that sites are under similar conditions, and only a few have addressed those site effects, particularly for tropical dry forests (Uhl *et al.* 1982, 1988, Moran *et al.* 2000, Powers *et al.* 2009, Mwampamba & Schwartz 2011, Dupuy *et al.* 2012). Since chronosequence's failure to project successional dynamics could be explained by subtle differences in site conditions, testing this assumption is relevant in explaining successional patterns and the usefulness of the chronosequence approach.

To advance our understanding of the power of age of abandonment and site conditions to explain and predict changes in forest attributes along succession, we developed a model-based analytical approach combining chronosequence and dynamic data to test chronosequence explanatory power and its predictions of successional dynamics. We then applied this procedure to study secondary succession of tropical dry forest (TDF) woody communities in abandoned cattle ranching pastures of western Mexico. Six different community attributes were analyzed: basal area, plant density, height, species richness, species evenness, and species composition. We further assessed the role of site factors like field management history, soil condition, and adjacent forest cover in explaining successional patterns of these attributes. Specifically, we tested the following: (1) whether age of abandonment is a major explanatory variable of among-site variability in community attributes and their observed net changes; (2) to what extent chronosequence models predict net changes in community attributes observed over 6 yr; and (3) to what extent site factors

other than age of abandonment explain variability in community attributes and their observed changes over time.

METHODS

ANALYTICAL APPROACH.—The main hypothesis behind the chronosequence approach is that time since field abandonment constitutes a major explanatory variable for differences in community attributes across sites. Testing this hypothesis commonly proceeds through fitting a statistical model relating the observed chronosequence data to age of abandonment (*i.e.*, a chronosequence model). If chronosequence assumptions were met (sites are under the same biophysical conditions and subjected to similar management regime), we would expect site dynamics to parallel the trajectory or present a trend similar to that predicted by the chronosequence model. Consequently, a test of the predictive power of a chronosequence could proceed by calculating observed community changes from repeated measurements over a given time period and comparing them with expected changes derived from the chronosequence model. Here, we develop and apply an analytical approach following this rationale.

The analytical approach can be summarized in seven steps. In step 1, a chronosequence model is fitted to explore if age of abandonment explains variability in attribute values among sites. In step 2, a confidence interval for the chronosequence model is calculated from a family of fitted models generated by bootstrapping samples. Step 3, expected net changes in attribute (NC_{exp}) are calculated from the chronosequence model as $NC_{exp} = A_t + \Delta t - A_s$, where A_t is the attribute value calculated from the model at a given age (time = t), and $A_t + \Delta t$ is the value of such a trait after Δt yr. Step 4, confidence intervals for the NC_{exp} are obtained by applying step 3 to the family of models from bootstrapped samples obtained in Step 2. Step 5, observed net changes in attribute (NC_{obs}) for each site are calculated as the difference between two repeated measurements separated by the Δt period. A 'net change model' relating NC_{obs} to age at first measurement is then fitted to explore to what extent age explains variability in observed net changes among sites. Step 6, test of the predictive power of the chronosequence on the observed successional dynamics is done by comparing the mean and confidence intervals for NC_{exp} (steps 3 and 4) with the net change model (step 5). Step 7, linear models are used to relate residuals from the chronosequence and net change models to site variables to assess the importance of site factors on succession beyond age effects. Further details on the analytical approach and an R code for its implementation are provided in Appendix S1.

TEST OF THE CHRONOSEQUENCE USING TROPICAL DRY FOREST DATA.—We applied the analytical approach to a case study of TDF secondary succession conducted in the Chamela-Cuixmala Biosphere Reserve (CCBR) and adjacent areas, on the Pacific coast of the state of Jalisco, Mexico (19°23'–19°30'N, 104°56'–105°04'W). Mean annual temperature is 24.6°C, and mean annual precipitation is 788 mm, with a severe drought season from November to May (García-Oliva *et al.* 2002). Because of rainfall

seasonality, most of the landscape is covered by TDF from 5 to 10 m high (Sanchez-Azofeifa *et al.* 2009). Areas adjacent to the CCBR have been transformed mainly into pastures for cattle raising during the past 40 yr (Maass *et al.* 2005). Those areas are often left without maintenance, resulting in the development of secondary forests (Burgos & Maass 2004).

A chronosequence was established with nine secondary forests from abandoned pastures and three old growth forests sites (without evidence of recent human disturbance). Sites were located at northwest and southeast extremes of the CCBR in order to include possible regional variations in climate or soils associated with geologic origin or topography (García-Oliva *et al.* 2002, Schaaf 2002). All of the sites were located on slopes (15° to 30°) to represent the dominant topographic condition (Balvanera *et al.* 2002, Cotler *et al.* 2002) and faced south (southeast to southwest) to represent the most extreme conditions in terms of high evaporative demand (Balvanera *et al.* 2002). All secondary forests were located in sites where land was used mainly for cattle ranching (from 4 to 28 yr after slash and burn of the former old growth forest) with repeated burning, planting of exotic grasses and free grazing. Age of abandonment varied between 0 and 12 yr by November 2004 (assessed through interviews with owners), when permanent plots were established and sites fenced with barbed wire to exclude cattle.

At each site a 20 m × 50 m plot was established. All woody plants including trees, shrubs and lianas, and arborescent cacti (henceforth all will be referred to as woody community) were tagged, identified and measured for diameter at breast height (dbh) in 2004 (we measured the diameter at the base for lianas, which will be hereafter referred to for all as dbh). Plant height was measured since 2007 (excepting lianas). A size-stratified sampling was used: stems with dbh ≥ 1 cm were sampled in half of the plot (10 m × 50 m) and those ≥ 2.5 cm dbh in the other half. Two additional censuses were carried out in 2007 and 2010 following the same sampling protocol.

For each plot and census year, we assessed structural attributes, as well as species diversity and species composition. Structural attributes included basal area, plant density and plant mean height (the latter only for plants with at least one stem > 2.5 cm dbh). Diversity attributes were rarefied species richness (for 50 individuals per plot) and evenness (using Hurlbert's Probability of Interest-specific Encounter), both calculated using EcoSim (Gotelli & Entsminger 2011). Species composition was reduced to a continuous scale by applying a non-metric multidimensional scaling ordination (NMDS) to a Chao-Sorensen matrix of dissimilarities for the data from the three censuses and 12 sites; site scores for the first ordination axis were then employed to represent species composition for each site/year combination. Stress value obtained was 0.021. NMDS was performed using the 'metaMDS' function in the vegan package for R (Oksanen *et al.* 2013).

Chronosequence models in step 1 were fitted using data from 2004. For each attribute, four different nonlinear models were tested: Michaelis-Menten, asymptotic, Gompertz and logistic (Table S1). In all models, old growth sites were included by setting their age as 100 yr, since model parameter estimates did not

change by more than 0.1 percent when old growth forest age varied between 50 and 500; other studies have used a similar criterion (Peña-Claros 2003, Becknell *et al.* 2012). Model fitting was performed using 'nls' function in R (R Core Team 2013). The best-fitted model for each community attribute was selected based on the AICc. For the net change models, the form of the model corresponded to the first derivative of the best-fitted chronosequence model (Table S1). Confidence intervals for model parameters were calculated based on 1000 bootstrapped samples for each model. Observed and expected net change (NC) in steps 3–5 were calculated for $\Delta t = 6$ for all attributes except mean plant height, in which case $\Delta t = 3$ yr.

Residuals from both the chronosequence models and the net change models were related to field management history, soil condition, and adjacent forest cover of the sites (step 6). Management previous to plot establishment, characterized through semi-structured interviews with landowners (Trilleras 2008), was summarized into variables describing the frequency, magnitude, intensity and duration of agricultural, pastoral and extractive activities (Appendix S3). Physical and chemical soil properties as well as soil degradation status were assessed from one soil profile in each site (Appendix S3; Trilleras 2008). Adjacent forest cover (by differentiating forested and non-forested areas) was quantified using true color imagery from 2003, downloaded from Google Earth[®] and interpreted using Arcmap[®] for buffers of 100–300 m (Appendix S3); these distances cover the spatial range at which most seed wind dispersal occurs (Contreras-Sánchez *et al.* 2011).

Site variables were subject to an ordination procedure to reduce their dimensionality and to ensure orthogonality. Ordination was performed using the 'dudi.mix' function in the ade4 package for R (Dray & Dufour 2007), which allows for the inclusion of continuous, ordinal and categorical data in the same analysis. Residuals from models were then related to ordination axes using linear models. The first three ordination axes, which explain 57.5 percent of variation in site variables, were tested (Table S2). We used the 'lmp' function in the lmPerm package for R (Wheeler 2010), which employs permutation tests to obtain *P*-values for the models without assuming normality. We included only the nine secondary forests in this analysis since management was meaningless for old growth forests. Finally, pairwise associations were tested among residuals from chronosequence models or net change models and those site variables that significantly correlated with the ordination axes. Associations were tested using Spearman correlations when site variables were quantitative or ordinal and correlation ratios when categorical. Because of the high number of site variables included in the analysis of pairwise associations (33 variables correlated to axis 1 through 3, shown in Table S2), an inflated probability of rejecting the general null hypothesis of no site effects could arise. Bonferroni corrections were then applied to *P* values of the pairwise associations in order to avoid this inflated probability.

TEST OF THE CHRONOSEQUENCE USING A SIMULATED DATASET.—We assessed the performance of the analytical approach by applying it to three different simulated repeated measurements' datasets

with known predefined properties. This allowed us to provide background for contrasting and discussing our results from real data. Dataset simulation was done by setting a logistic chronosequence model and then generating random values from it, which constituted initial (chronosequence) observations for different sites. Simulated trajectories for each of these sites were then created based on the expected trajectory defined by the chronosequence model. We allowed for variation in one of three criteria: (1) sample size; (2) amount of random variation in site trajectories; and (3) degree of systematic departure of observed trajectories from those expected from the chronosequence model. Performance of the analytical approach was assessed as described before (see step 6 above). Further details on simulation and their results are shown in Appendix S2.

RESULTS

AGE OF ABANDONMENT AS AN EXPLANATORY VARIABLE OF COMMUNITY ATTRIBUTES AND THEIR OBSERVED CHANGES.—Chronosequence models showed that age of abandonment had a high explanatory power for all of the six attributes of the TDFs. Overall, age explained 60–97 percent of the differences in community attributes across sites (Table 1A). Structural attributes, namely basal area, plant density and mean plant height, were better explained by age ($R^2 = 0.79$ – 0.97) than were species richness,

evenness and species composition ($R^2 = 0.60$ – 0.80 ; Fig. 1; Table 1A). Basal area and plant density showed a sigmoid trajectory (Fig. 1A and B), while the other attributes exhibited a more asymptotic one (Fig. 1C–F).

Observed net changes in community attributes (NC_{obs}) were partially explained by age of abandonment (Table 1B). Age explained NC_{obs} better for species richness, evenness and composition ($R^2 = 0.53$ – 0.57) than for structural attributes ($R^2 = 0.06$ – 0.40). Net change models for basal area and plant density described a humped pattern in relation to age (Fig. 2A and B), while those of other attributes describe a negative trajectory (Fig. 2D–F). The NC_{obs} for mean plant height did not show any relation to age (Fig. 2C; Table 1B).

CHRONOSEQUENCE POWER FOR PREDICTING OBSERVED ATTRIBUTE CHANGES.—Net change models for the woody communities in the TDFs described successional trajectories that fell consistently below the expected trajectories for basal area, plant density, mean height, and species composition (Fig. 2). On the contrary, the NC_{obs} trajectory for evenness was consistently above the expected one. Overestimation was significant for two structural attributes, basal area and mean plant height, as trajectories defined by their net change models fell outside confidence intervals of the NC_{exp} trajectories (Fig. 2A and C). In contrast, chronosequence attribute models adequately predicted those NC_{obs}

TABLE 1. Parameters and statistics for (A) chronosequence models testing the effects of age of abandonment on attribute inter-site variation and (B) net change models testing the effects of age of abandonment on recorded changes of community attributes of secondary tropical dry forest woody communities in abandoned pastures and old growth forest sites in western Mexico. Chronosequence models were adjusted using 2004 data. Observed net changes in attributes correspond to the 2004 through 2010 period. Model refers to the form of the fitted model, with a, b, c, α , β , and γ being model parameters; see Table S1 for model and parameter definitions. RSE is residual standard error, and R^2 is coefficient of determination. Parameters in bold are those testing the effect of age of abandonment.

(A) Chronosequence models ^a						
Attribute	Model	a	b	c	RSE	R ²
Basal area	Gompertz	21.24**	4.29**	0.80**	1.69	0.97
Plant density	Logistic	6044**	5.51**	2.38**	822	0.91
Height	Logistic	5.93**	−0.75	5.69**	0.616	0.79
Rarefied richness	Logistic	24.87**	1.16	4.44**	2.86	0.80
Evenness	Logistic	0.94**	−15.02**	6.89**	0.031	0.60
Composition	Logistic	1.39**	4.91*	5.11**	0.279	0.71

(B) Net change models ^b						
Observed change	Model	α	β	γ	RSE	R ²
Basal area	Gompertz	38.12**	3.56**	0.56**	2.40	0.32
Plant density	Logistic	13320**	2.42	0.79**	1380	0.40
Height	Logistic	1.06	6.28**	1.09**	0.044	0.06
Rarefied richness	Logistic	95.4**	2.63	3.84**	2.27	0.57
Evenness (PIE)	Logistic	1.32*	−1.13	5.92*	0.002	0.53
Composition	Logistic	1.86**	5.56*	2.53**	0.081	0.53

Significance levels are ** $P < 0.01$ and * $P < 0.05$.

^aModels fitted to community attributes were selected on the basis of minimization of AICc from four possibilities: Michaelis-Menten, Asymptotic, Gompertz, and Logistic.

^bModels fitted to observed net changes correspond to the first derivatives of selected chronosequence models.

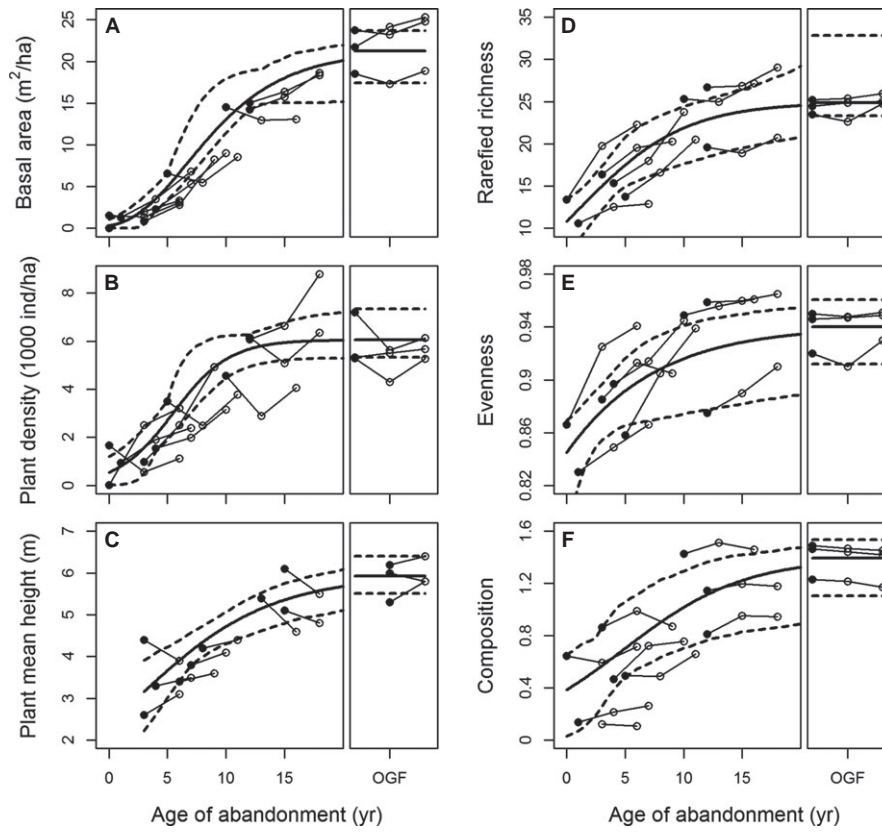


FIGURE 1. Woody community attributes as a function of age of abandonment of secondary tropical dry forest (TDF) in the Chamela-Cuixmala region, western Mexico. Attribute values for the same site in different years are linked with solid thin lines. Black dots represent community values for 2004 (2007 for plant mean height), and white dots are values for 2007 and 2010. Black, continuous thick lines represent chronosequence models fitted to black dots (as in Table 1) and dotted lines their percentile-based, 95% CI limits. OGF refers to old growth forest sites.

trajectories for two species-based attributes: rarefied richness and species composition (Fig. 2D and F). NC_{obs} trajectories for plant density and species evenness fell partially inside the confidence interval (Fig. 2B and E).

SITE FACTORS INFLUENCING SUCCESSION.—Ordination axes derived from site factors did not explain residuals from chronosequence models, but partially explained residuals from some net change models (Table 2). The residuals of the model for net changes in mean height were related to ordination axis-3 (Table 2), which in turn was linked to different aspects of forest clearing, cattle grazing regime, and extraction of timber (Table S2). Residuals of the models for net changes in species richness and composition were related to ordination axis-2 (Table 2), which was related to different aspects of field management, cattle activity, soil condition, and adjacent forest cover (Table S2). For these three net change model residuals, we found significant correlations with site variables associated with ordination axes-2 and 3 (Fig. 3). For mean plant height, residuals increased as years since last slash increased (Fig. 3A). Residuals from species richness decreased as the extension of forest clearing increased or when no herbicide was applied for weed control (Fig. 3B and C). Finally, residuals from species composition decreased as the duration of cattle grazing

and timber extraction duration and extension increased (Fig. 3D–F). Adjacent forest cover variables did not show any significant association with residuals, although coverage in 200 and 300 m buffers were associated with axis-3 (Table S2). Adjacent forest cover variables were highly correlated with age of abandonment (Spearman rank correlation coefficients = 0.63 ($P < 0.01$), 0.70 ($P < 0.05$), 0.77 ($P < 0.05$) for buffer areas of 100, 200 and 300 m radius, respectively).

PERFORMANCE OF THE ANALYTICAL APPROACH USING SIMULATED DATASETS.—Both the amount of random or systematic error in site trajectories caused significant and consistent divergence between observed and expected net changes (Figs. S2 and S3). Variation in sample size had less effect on divergence between chronosequence and dynamic approaches, with small sample sizes sometimes leading to partial departure from chronosequence expectations (Fig. S1).

DISCUSSION

AGE OF ABANDONMENT AS EXPLANATORY VARIABLE OF COMMUNITY ATTRIBUTES AND THEIR OBSERVED CHANGES.—Age of abandonment was clearly a major factor explaining variation in community attri-

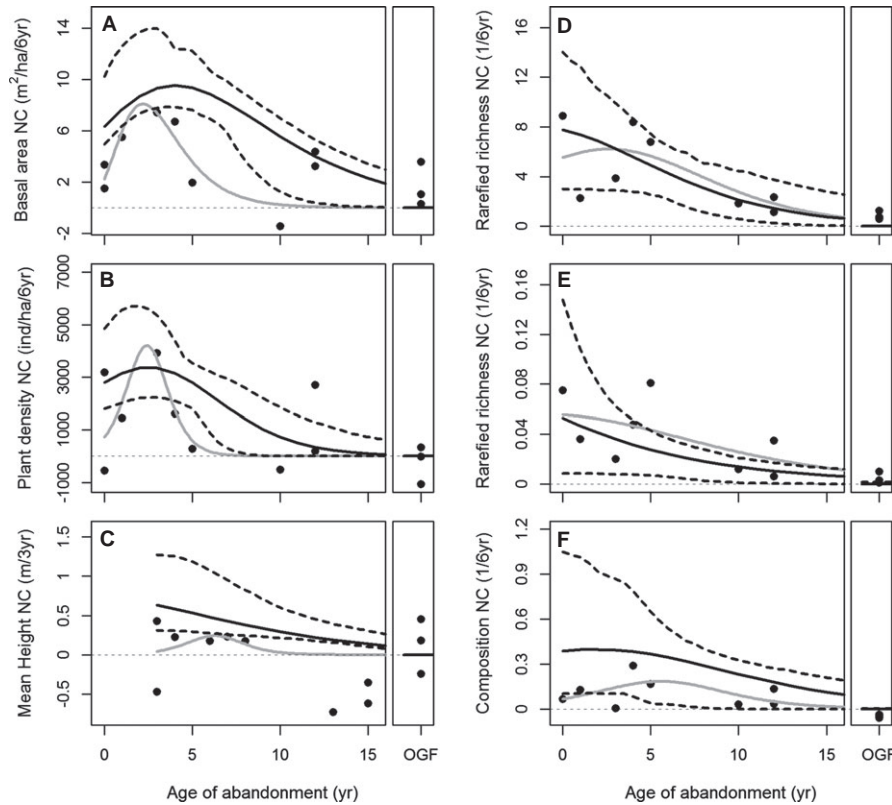


FIGURE 2. Net changes (NC) in community attributes as a function of age of abandonment of secondary tropical dry forests in the Chamela-Cuixmala region, western Mexico. Dots represent observed net changes for each site, calculated for the 2004 through 2010 period (2007–2010 for plant mean height). Gray continuous lines represent the net change models fitted to observed changes. Black continuous lines represent expected attribute changes from chronosequence models fitted to community attributes (see Fig. 1), with dotted lines being their 95% CI limits. OGF refers to old growth forest sites.

but based on chronosequence data in secondary TDFs in Chamela. Similar results have been observed in other chronosequence-based studies where sites were selected with similar criteria, *i.e.*, seemingly homogeneous environmental and historic conditions (Peña-Claros 2003, Lebrija-Trejos *et al.* 2010, Muñoz-Castro *et al.* 2011). The explanatory power of age, however, varied with the attribute analyzed: it was higher for structural attributes than for diversity and composition. Structural attributes have been shown to recover independently from the number or identity of species and to be less susceptible to deviation from the expected successional trajectory defined by age (Pascarella *et al.* 2000, Molina-Colon & Lugo 2006, Marin-Spiotta *et al.* 2007). Perhaps once a minimum set of species spanning over a range of functional responses is present, the recovery of forest structure proceeds in a more deterministic way, only loosely associated with the number or identity of species (Yachi & Loreau 1999, Lasky *et al.* 2014). The addition of new species seems necessary, though, to sustain forest recovery over time (Allan *et al.* 2011).

Age of abandonment also explained variation in dynamic data, *i.e.*, observed attribute net changes across sites, but with lower explanatory power than for community attributes. Differences in explanatory power may be related to the effect of water

availability at different time scales. Regarding rates of change, the study of the seedling community in the same chronosequence has shown that they are not related to age but rather to interannual variation in precipitation patterns (Maza-Villalobos *et al.* 2011, 2013). In the case of community attributes, studies of the conserved forest show that they are clearly correlated with

TABLE 2. Linear models testing for the effects of site factors on residuals from chronosequence models and net change models shown in Table 1. Only those residuals with significant effects are shown. Site variables assessing management history, soil condition, and adjacent forest cover (see Appendix S3) were reduced to three ordination axes (A1–A3) which were further included in the models. The Coef *i* column refers to model parameter relating residuals and age of abandonment. RSE is residual standard error, R² is coefficient of determination and NC_{obs} are observed net changes. Significance codes** are ***P < 0.01 and *P < 0.05

Model residuals	Axis	Coef <i>i</i>	RSE	R ²
Height NC _{obs}	A-3	0.039*	0.051	0.44
Richness NC _{obs}	A-2	0.277*	0.273	0.58
Composition NC _{obs}	A-2	0.009*	0.010	0.51

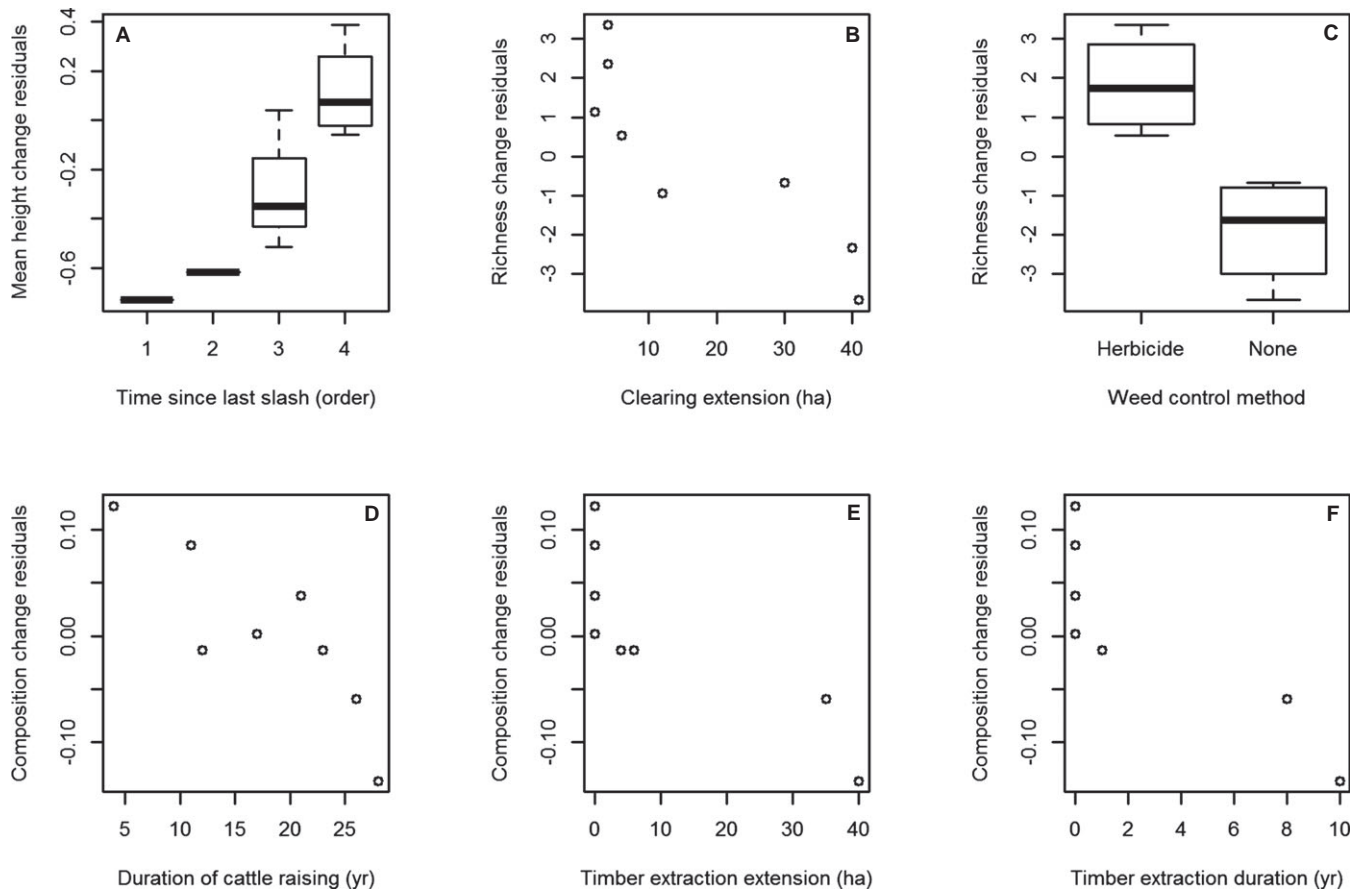


FIGURE 3. Pairwise relationships between residuals from chronosequence models or net change models and site variables assessing management history, soil condition, and adjacent forest cover in secondary tropical dry forest (TDF) from the Chamela-Cuixmala region, western Mexico. Only those residuals and site variables significantly associated with ordination axis explaining them are shown; $P < 0.05$, Bonferroni corrected Spearman rank correlation tests). See Table 2 and text for further details.

topographically driven differences in water availability (Lott *et al.* 1987, Segura *et al.* 2003). It then seems that while net changes in attributes may respond to short-term (interannual) water availability, which is highly variable and not related to age, community attributes could be representing the effect of historical average water availability captured by age of abandonment.

MATCH BETWEEN OBSERVED AND PREDICTED CHANGES IN COMMUNITY ATTRIBUTES THROUGH TIME.—Our results suggest that chronosequence models have less power to predict short-term successional dynamics for forest structural attributes than for species identity-based attributes like diversity or composition. The two attributes significantly and consistently overestimated by chronosequence models, namely basal area and mean plant height, are structural attributes. The third structural attribute (plant density) was also overestimated along all the age range evaluated, although not significantly. On the contrary, species-based attributes were not significantly over- or underestimated, although species evenness and composition net change models fell partially outside intervals predicted from chronosequences.

These results contrast with the explanatory power of the chronosequence models, for which structural attributes like basal area and plant density had higher R^2 values, but did not perform better in predicting observed net changes than species-based models like evenness and composition with lower R^2 . Therefore, there seems to be no relation between R^2 values of the chronosequences and their predictive power. These findings contradict the generalized view that chronosequence models predict changes of structural attributes, particularly basal area, better than those of diversity or taxonomic composition (Chazdon *et al.* 2007, Quesada *et al.* 2009). This view is mostly based on the commonly high R^2 values found for structural variables when using chronosequence approaches. Other studies, however, have also shown wide variation in the predictive power of the chronosequences with strong departures of the observed from the expected trajectories (Breugel *et al.* 2006, Chazdon *et al.* 2007, Feldpausch *et al.* 2007) as well as close matches (Foster & Tilman 2000, Lebrija-Trejos *et al.* 2010). Therefore, ours and other studies show that the power of chronosequence models to predict short-term dynamics in successional forest may be site- or even

attribute-dependent and should not be deduced from their explanatory power.

The possibility of a mismatch between chronosequences and dynamic approaches has potential implications for the application of the chronosequence approach to practical situations. For example, biomass and carbon stock recovery through succession in tropical forests is commonly inferred from forest structural measurements done along a chronosequence (Vargas *et al.* 2007, Yang *et al.* 2011, Becknell *et al.* 2012). As previously shown, however, net changes of structural attributes derived from chronosequences can be quite dissimilar from those observed through repeated measurements, making biomass and carbon recovery estimations significantly biased. Our findings therefore indicate the need for caution in the application of chronosequence data in evaluations of ecosystem service recovery.

INFLUENCE OF SITE FACTORS ON SUCCESSION.—In our study, sites were selected to conform a chronosequence based on their location on similar biophysical conditions and to include the dominant field management features in the study region (Burgos & Maass 2004). Our results show, however, that variation in community dynamics is related to site factors, mainly those associated with field management previous to abandonment, even after accounting for the effect of age of abandonment. Such results suggest that field management history affects successional processes. In general, the higher residuals from net change models were associated with low extension or duration of field management and time since forest clearing (Fig. 3). An exception to this pattern was the higher residuals of the net changes model for richness found in sites where herbicide was applied. Thus, our results are in general concordance with previous findings about reduced successional recovery under more severe field management (Uhl *et al.* 1988, Moran *et al.* 2000, Zarin *et al.* 2005, Molina-Colon & Lugo 2006). An interesting implication of these results is the complexities involved in site selection for chronosequences: an assessment of management history is required to guarantee that sites have very similar management histories or, even better, that information is included during chronosequence data analysis. Further work is needed to more strongly support these findings by increasing sample size of plots and by including more contrasting field management conditions.

It is also interesting that both soil properties and adjacent forest cover did not show any association with the observed successional dynamics, although they were related to ordination axes-2 and 3. The limited contribution of soil conditions contrast with the sharp mosaic in geological origin found in the region (Cotler *et al.* 2002). Our results, though, concur with previous studies that showed that old growth TDF structure and diversity in the region is not affected by the type of geology and soil (Durán & Meave 2006), but rather by water availability, associated to the slope and position in the landscape (Balvanera *et al.* 2002). The lack of association between adjacent forest cover and model residuals could be explained by inadequate sampling or by the correlation between adjacent forest cover and age of abandonment. Our sample was not designed to test the effect of the sur-

rounding landscape matrix features on site dynamics, so the lack of association could simply be the result of inadequate representation of the complete range of forest coverage around sites. On the other hand, we also found a significant correlation between age and forest cover, which we speculate could result from the spatial autocorrelation of management practices (Helmer *et al.* 2008, Crk *et al.* 2009). This correlation could imply that when testing the effect of age of abandonment, we may not only have tested the intrinsic processes of development of the forest, *i.e.*, plant growth, but also the potential effect of extrinsic factors like increased seed rain and seedling establishment associated with increased adjacent forest cover, as has been previously shown (Maza-Villalobos *et al.* 2011).

SAMPLE SIZE LIMITATIONS AND PERFORMANCE OF THE ANALYTICAL APPROACH.—Our conclusions could be limited by the small sample size of the tropical dry forest dataset (nine secondary forest sites). Results from the analysis of these data, however, are consistent with the performance of the analytical approach under simulated conditions. NC_{exp} trajectories observed for those community attributes with significant departure from expectations (basal area and mean height) are more consistent with a systematic departure of observed trajectories from chronosequence models than with a spurious effect caused by small sample size. Although small sample sizes caused a partial departure from chronosequence expectations during simulations, the analytical approach is relatively robust to sample size. Instead of causing the spurious rejection of chronosequence expectations, small sample size seems to be related to the reduced power of the test, since prediction intervals become wider as sample size reduces. On the contrary, simulations testing the effect of the degree of systematic departure between observed and expected NC show the test is sensitive to this parameter. Increased random deviation also results in higher divergence between observed and expected results (Appendix S2). Overall, simulations suggest that the analytical approach is sensitive to deviation in successional trajectories with respect to chronosequence model expectations.

We believe the analytical approach developed here has clear advantages beyond low sensitivity to sample size. Previous studies have tested the match between chronosequence and dynamic approaches by correlating predicted rates from a chronosequence model to observed rates (Maza-Villalobos *et al.* 2011). This constitutes a ‘coarse test’ of the chronosequence, since correlation can occur even when observed and expected rates show a different kind of relationship with time and, therefore, come from quantitatively different relationships between age and community attributes. In addition, correlations between age and observed rates do not actually test chronosequence predictions, as exemplified here by basal area, where the NC_{obs} were significantly related to fallow age, but the chronosequence model failed to predict them (*e.g.*, Foster & Tilman 2000). Instead, our approach allowed us to test for specific predictions about expected community changes derived from specific statistical models fitted to community attributes. Its implementation in other chronosequence

datasets will allow further assessments of its advantages and shortcomings.

CONCLUSIONS

We found that although age of abandonment has a high explanatory power for differences in community attributes of secondary TDFs, the predictive power of chronosequence models can be poor and not related to its explanatory power. Part of the mismatch between observed and expected net community changes over 6 yr may be caused by temporal environmental conditions affecting short-term successional dynamics, although differences in management history among sites could also influence such disparity. Our results point out the need to integrate chronosequence and dynamic approaches to better understand and predict secondary succession. Furthermore, they suggest that caution is needed when applying chronosequences to the evaluation of ecosystem services recovery. By providing an analytical approach to statistically test both the explanatory and predictive power of chronosequences, we have advanced in the integration of different approaches to study succession and, therefore, in the recognition of their possibilities and limitations.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURES S1 and S2. Expected net changes in attribute and their 95% CI limits in relation to age of abandonment.

FIGURE S3. Observed attribute net changes and the corresponding trajectory for the net change model.

FIGURE S4. Comparison between expected net changes predicted from chronosequence and those observed from dynamic data.

FIGURE S5. Simulation results for sample size variation.

FIGURE S6. Simulation results for variation in randomness of observed changes.

FIGURE S7. Simulation results for variation in the degree of systematic departure between observed changes and expected changes.

TABLE S1. *Nonlinear models used to test the effects of age of abandonment on community attributes and their observed net changes for secondary tropical dry forests in abandoned cattle pastures and old growth forest sites in western Mexico.*

TABLE S2. *Site variables associated with ordination axes summarizing field management history, soil condition, and adjacent forest cover of secondary tropical dry forest woody communities in abandoned pastures in western Mexico.*

APPENDIX S1. Analytic procedure to explore the power of chronosequences to explain and predict successional changes based on repeated measurements.

APPENDIX S2. Simulations for assessing the performance of the analytical approach to test chronosequence predictions based on the repeated measurements data.

APPENDIX S3. Site factors beyond age of abandonment explaining community attributes and observed net changes.

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