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Cambios funcionales en la vegetación del Bosque Tropical Seco de la región Chamela-Cuixmala en respuesta a huracanes de alta intensidad.

TESIS

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PRESENTA

Diana Laura Jiménez Rodríguez

TUTORA DE TESIS: Dra. Mariana Yolotl Alvarez Añorve

COTUTOR: Dr. Luis Daniel Avila Cabadilla

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PRESENTE

Por medio de la presente me permito informar a usted que en la **sesión ordinaria 13** del **H. Consejo Técnico** de la Escuela Nacional de Estudios Superiores (ENES) Unidad Morelia celebrada el día **22 de noviembre del 2018**, acordó poner a su consideración el siguiente jurado para la presentación del Trabajo Profesional del alumno **Diana Laura Jiménez Rodríguez** de la Licenciatura en **Ciencias Ambientales,** con número de cuenta **413087829**, con el trabajo titulado: "Cambios funcionales en la vegetación del Bosque Tropical Seco de la región Chamela-Cuixmala en respuesta a huracanes de alta intensidad" bajo la dirección como **tutora** de la Dra. Mariana Yólotl Álvarez Añorve y como **co-tutor** el **Dr. Luis Daniel Avila Cabadilla**.

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Sin otro particular, quedo de usted.

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
Morelia, Michoacán a, 31 de enero del 2018.

DR. VÍCTOR HUGO ANAYA MUÑOZ
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Índice

Resumen

Los bosques tropicales secos (BTS) no solo están bajo presión de las actividades humanas, sino que hay una gama de disturbios que los afectan continuamente. A la urbanización, incendios provocados y remoción de la cubierta arbórea para el desarrollo de actividades agropecuarias, se suman perturbaciones naturales tales como tormentas, incendios o huracanes, siendo estos últimos los más frecuentes La actuación conjunta de diversos disturbios tanto naturales como de origen humano, está determinando la dinámica de estos bosques, creando complejos patrones espaciales en la estructura y composición de la vegetación.

Dado que el cambio climático podría provocar un aumento en la intensidad de huracanes en la costa del Pacífico Mexicano, y esta región está dominada por un BTS altamente diverso, mismo que está inmerso en un paisaje antropogénico, esta zona es un modelo ideal de estudio para evaluar los efectos del aumento en la intensidad de huracanes en la vegetación tropical tanto en bosques conservados como en bosques previamente impactados por la actividad humana (bosques secundarios).

El objetivo de este estudio fue justamente el comparar, en la costa del Pacífico Jaliscience, la vegetación de los bosques conservados y secundarios del bosque tropical seco, en términos del nivel de daño sufrido por un huracán de alta intensidad y su capacidad de recuperación, así como identificar parámetros (asociados a la composición, estructura y función) que pudieran estar relacionados tanto con el daño sufrido como con la capacidad de recuperación de dicha vegetación. Específicamente, en esta tesis evaluamos, antes y después del paso del huracán Patricia (categoría 5 en la escala de Saffir-Simpson), la composición específica de la vegetación (atributos florísticos) y sus atributos estructurales (área basal, altura, número de ramas, densidad de individuos, índice de área foliar). Posteriormente al paso del huracán se evaluó también el tipo y nivel de daño sufrido por la vegetación (*sensu* Vandecar et al., 2011 y Navarro-Martínez et al., 2012), sus atributos funcionales foliares (contenido de clorofila, grosor, área foliar específica, masa fresca foliar) y su capacidad de rebrote (número y área basal de los rebrotes) como un *proxi* de la capacidad de regeneración. Estos atributos se evaluaron en 3732 individuos de 279 especies arbóreas, ubicados en un total de ocho parcelas (4 de bosque secundario y 4 de bosque conservado), cada una de 1000 m^2 (50x20 m).

Respecto a la estructura de la vegetación, se encontró que el mayor número de árboles muertos, árboles desenraizados y árboles doblados correspondían a los individuos de mayor altura y área basal, localizados en bosques donde los árboles emergentes eran más altos (bosques conservados). Además, se encontró que el mayor número de árboles con troncos rotos o inclinados así como con ramas secundarias rotas, estuvieron asociados a áreas con un mayor índice de área foliar y una mayor densidad de individuos. El daño más común para ambos tipos de bosque fue “tronco inclinado” seguido de “tronco doblado” en

el bosque conservado, y de “ramas secundarias rotas” en el bosque secundario. Por otra parte, la mayor proporción de individuos muertos se encontró en el bosque conservado (8.46%). Mientras que el bosque secundario presentó una mayor proporción de individuos sin daños (11.01%).

En cuanto a la capacidad de rebrote, se detectó que el mayor porcentaje de individuos que producen un alto número de rebrotes (>30 rebrotes) se encontraron en el bosque conservado, mientras que el mayor porcentaje de individuos que producen un número reducido de rebrotes (<10 rebrotes) se encuentra en el bosque secundario. Adicionalmente, se encontró que en ambos bosques (conservado y bosque secundario) los árboles más altos y con mayor área basal son quienes producen menor cantidad de rebrotes. La capacidad de rebrote estuvo también asociada a atributos funcionales foliares como el contenido de clorofila y la densidad foliar, indicando que dicha capacidad está asociada a una alta capacidad fotosintética.

Nuestros resultados sugieren que en escenarios de aumento en la frecuencia y/o intensidad de huracanes en la costa del Pacífico Mexicano, este BTS podría cambiar su fisonomía hacia un dosel más bajo dominado por árboles de menor altura y diámetro. Asimismo, la proporción de especies con resistencia al daño mecánico y alta capacidad de rebrote (especies de tallas pequeñas con tejidos productivos y resistentes) podría incrementarse.

Este estudio nos permitió el impacto de un huracán de alta intensidad en la vegetación del BTS y en qué medida los atributos evaluados se relacionan con el nivel de daño sufrido y la capacidad de rebrote de las diferentes especies presentes tanto en bosques conservados como en bosques secundarios. Estas relaciones, a su vez, nos brindaron información sobre las bases funcionales de la respuesta de la vegetación y pueden ser útiles para predecir como cambiarán los atributos de este BTS ante un aumento en la frecuencia de este tipo de huracanes. Finalmente, este tipo de información también puede constituir una base teórica para generar estrategias de manejo que ayuden al bosque y a las poblaciones humanas que habitan a los alrededores a evitar futuros riesgos.

Abstract

The Tropical Dry Forests (TDF) are altered by anthropogenic activities as well as by natural disturbances that frequently affect them. Besides urbanization, provoked fires, and plant cover removal, TDF are affected by storms and hurricanes, which are the most frequent type of natural disturbance in this ecosystem. The synergic effect of anthropogenic and natural disturbances are determining the forest dynamics creating complex spatial patterns in structure and vegetation composition.

Provided that climatic change could cause an increase in the intensity of the hurricanes in the Pacific Coast of Mexico, and that this region is dominated by a highly diverse TDF which is immerse in an anthropogenic landscape, this zone is ideal for evaluating the effects of the increase in the hurricanes intensity on tropical vegetation, specifically, in conserved and anthropogenically disturbed forests (secondary forests).

The objective of this study was to compare, in the Pacific coast of Jalisco (México), the vegetation of conserved and secondary TDF in terms of the level of damage caused by a high intensity hurricane and of its recovering capacity. We also aimed to identify parameters (floristic, structural and functional) related to the level of damage and to the recovering capacity of the vegetation. Specifically, in this thesis we evaluated, before and after the hurricane Patricia (category 5 in the Saffir-Simpson scale), the floristic (species composition) and structural (basal area, height, number of branches, stem density, leaf area index) attributes of the vegetation. After the hurricane we also evaluated the type and level of damage suffered by the vegetation (sensu Vandecar et al., 2011 y Navarro-Martínez et al., 2012), its functional attributes (chlorophyll content, leaf thickness, specific leaf are, leaf fresh mass) and its resprouting capacity (resprouts number and basal area) as a proxy of the recovery capacity. These attributes were evaluated in 3732 individuals of 279 woody species located in eight 1000m2 plots (4 plots of secondary forest and 4 plots of conserved forest).

Regarding the structure of the vegetation, it was found that the highest number of dead trees, uprooted trees and bent trees were those with the highest height, and the largest basal area, growing in forests with taller canopies (i.e. conserved forests). In addition, it was found that the greatest number of trees with broken or inclined trunks as well as with broken secondary branches, were associated to sites with a higher leaf area index, higher density of individuals and smaller distance between individuals. The most common type of damage for both forests was “inclined trunk” followed by “bent trunk” in the conserved forests and by “broken secondary branches” in the secondary forests. Moreover, the highest proportion of death individuals was found on OGF (8.46%), while the SF presented a higher proportion of undamaged trees (11.01%).

Regarding the resprouting ability, it was detected that the highest percentage of individuals that produce a higher number of resprouts (> 30 resprouts) were found on the OGF, while the higher percentage of individuals that produce a reduced number of resprouts (<10 resprouts) were found on the secondary forest. Additionally, it was found that in both types of forest (conserved and secondary), those trees with both highest height and basal area, are producing a lower proportion of resprouts. Resprouting ability was also associated to leaf functional traits such as chlorophyll content and leaf density, indicating a greater biomass acquisition in species with higher photosynthetic capacity.

These results suggest that in scenarios of increasing frequency and/or intensity of hurricanes, the TDF of the Pacific Coast of Mexico could change their physiognomy toward a canopy of lower height with trees of lower diameter in average. The proportion of species with strategies resistant to damage and favoring recovery (i.e smaller sizes, productive and resistant tissues) could increase as well.

This study allowed us to characterize the impact of a high intensity hurricane in the TDF vegetation, and to what extent the evaluated attributes are related to the level of damage of the vegetation and to its resprouting capacity in preserved and secondary forests. These relationships provided us information about the functional basis of the vegetation response and could be useful to predict how the attributes of this TDF would change with an increase in the frequency of this type of hurricanes. Finally, this information could also constitute a theoretical basis for management strategies focused on preventing future risks for the forest and the human communities associated to this system.

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CAPÍTULO I

Introducción general

1. INTRODUCCIÓN

Un disturbio puede ser definido como cualquier evento de origen natural o antrópico que interrumpa el ecosistema, la comunidad o la estructura de la población y cambie los recursos o el entorno físico (White y Pickett 1985). Tal es el caso de los huracanes (también llamados ciclones tropicales o tifones), que son un tipo de tormenta que se forma sobre aguas tropicales o subtropicales (Baker, 1992; NOAA, 2017). Las tormentas con vientos sostenidos menores a 62.7 km/h son llamadas depresiones tropicales, las que presentan vientos máximos sostenidos mayores a 62.7 km/h, son llamadas tormentas tropicales, y las que llegan a tener vientos sostenidos máximos de 119 km/h, son llamadas huracanes. La clasificación de un huracán está basada en la escala Saffir-Simpson, que tiene un rango o categoría del 1 al 5 basada en la velocidad máxima de los vientos sostenidos (NOAA, 2017).

Los huracanes juegan un papel importante en el clima del planeta. Su formación, tamaño, intensidad y movimiento son influidos por el balance de calor de la tierra (Baker, 1992). Hay estudios que indican un aumento en la intensidad y frecuencia de huracanes a nivel global (Knutson et al., 2015), a partir de simulaciones a futuro de la intensidad y frecuencia de huracanes a nivel global. Los resultados indican que hay una probabilidad del 3.6% de observar un aumento en la intensidad de huracanes (categoría 1 a 5) y tormentas tropicales. De acuerdo a este estudio, la región del noroeste del Pacífico posee la mayor probabilidad de incremento de intensidad, con un aumento del 8% en la intensidad de los huracanes. Dicha región incluye parte de la costa del pacífico mexicano.

Una gran parte de la vegetación ubicada en las costas del Pacífico Mexicano corresponde al Bosque Tropical Seco también llamado Selva Baja Caducifolia, Selva Baja Subcaducifolia, o Bosque Tropical Caducifolio, dependiendo de la clasificación aplicada (Miranda y Hernández, 1963; Rzedowski, 1978). Dicha vegetación, podría experimentar los efectos derivados del aumento en la intensidad y frecuencia de huracanes de acuerdo a la información obtenida por Knutson et al (2015).

Los huracanes pueden cambiar las características del suelo y la vegetación en grandes áreas, e influir en la economía y calidad de vida de las sociedades humanas en las zonas afectadas (Baker, 1992). En el caso específico de la vegetación, estos fenómenos meteorológicos pueden ejercer un profundo impacto en su estructura (altura promedio, diámetro promedio del tronco), así como en su fenología, productividad y patrones de reproducción (O'Brien, 1992), Por lo tanto diversos estudios se han enfocado en explorar el impacto de los huracanes en la vegetación, evaluando su nivel de cambio y las posibles consecuencias del mismo (Thopmson et al, 2007, Bonilla-Moheno, 2010; Vandecar et al, 2011; Cole et al, 2014; Valdéz-Hernández et al, 2014; Webb et al, 2014; Holm et al, 2017; Wang et al, 2017; Zhang et al, 2017).

1.1 El Bosque Tropical Seco

Los Bosques Tropicales y Subtropicales Secos son ecosistemas que se distribuyen entre los 20°de latitud norte y 20º de latitud sur, se encuentran por debajo de los 1200 msnm y representan en total 130 740 587 km^2 de la superficie terrestre. El 8.8% de este total se distribuye en América Latina y el Caribe (Bezaury, 2010; Ceballos et al, 2010). En general, estos bosques representan cerca de un 42% de los bosques tropicales del mundo (Holdrige

1967). Se caracterizan por tener hasta 7 u 8 meses de sequía, época durante la cual, la mayoría de la vegetación pierde entre el 50 y 100% de las hojas (Challenger y Soberón, 2008; Bezaury, 2010;).

En México, los BTS cubren aproximadamente el 11.26% de la superficie del país (Challenger y Soberón, 2008). En la costa del pacífico se distribuyen desde Baja California Sur y Sonora hasta Chiapas. Hay otras regiones del país en donde también se desarrollan estos bosques como Tamaulipas y el sureste de San Luis Potosí, en el norte y centro de Veracruz, y en el norte de la península de Yucatán (Noguera et al. 2002). Es altamente diverso florísticamente y en conjunto con los bosques tropicales subcaducifolios alberga aproximadamente el 20% de la flora de México, de la cual el 40% corresponde a especies endémicas (Rzedowski 1991; Noguera et al 2002). Uno de los BTS más diversos a nivel continental se encuentra en las costas del Pacífico en Jalisco y Michoacán (Gentry, 1995).

Los BTS también constituyen uno de los ecosistemas tropicales más amenazados del mundo (Sanchez-Azofeifa et al., 2005). En la vertiente del Pacífico, por ejemplo, se encuentran aproximadamente 142,000 km^2 de bosque seco que corresponde a un 53% de la cobertura original del BTS, es decir, dicha vertiente ha perdido el 46% de su cobertura (Trejo, 2010).

La costa del Pacífico sufre el efecto de los fenómenos de ENSO (El Niño Southern Oscilation) y “La Niña” que, por lo general, influyen en los volúmenes anuales de precipitación (Durán, 2004). Dado que el cambio climático podría provocar un aumento en la intensidad de huracanes en esta zona, este aumento podría actuar sinérgicamente con la perturbación antropogénica ya existente, que ha sido provocada principalmente por prácticas ganaderas y agrícolas que se implementaron a gran escala en la zona desde hace aproximadamente tres décadas (Sanchez-Azofeifa et al., 2009).

Las consecuencias de la acción sinérgica de perturbaciones naturales y antropogénicas, así como los mecanismos de regeneración de la vegetación, deben ser estudiadas a profundidad en sistemas tropicales tan diversos y amenazados como el BTS. En este sentido, cabe señalar que los mecanismos de sucesión y regeneración de este tipo de vegetación aún están escasamente descritos (Quesada et al., 2013). Entender estos procesos ecológicos en el contexto actual, nos podría ayudar a saber cómo estos sistemas responden ante las perturbaciones tanto naturales como antrópicas, y de esta forma poder planear o mejorar estrategias de manejo y conservación para evitar futuras pérdidas de biodiversidad.

1.2 Los disturbios naturales en los bosques tropicales

Los BTS no solo están bajo presión de las actividades humanas, sino que hay una gama de disturbios que los afectan continuamente. A la urbanización, incendios provocados y remoción de la cubierta arbórea para el desarrollo de actividades agropecuarias, se suman perturbaciones naturales tales como tormentas, incendios o huracanes, siendo estos últimos los más frecuentes (Navarro-Martínez et al., 2012). La actuación conjunta de diversos disturbios tanto naturales como de origen humano, está determinando la dinámica de estos bosques, creando complejos patrones espaciales en la estructura y composición de la vegetación, que actualmente consiste en una matriz de tierras agrícolas en uso, tierras agrícolas abandonadas que han dado origen a bosques secundarios en distintos estadios de sucesión y parches de bosque conservado. Esta matriz define tanto la configuración como la composición del paisaje (Chazdon, 2003).

Cuando el dosel de la vegetación es afectado por un huracán, la recuperación de la estructura y composición del bosque es más rápida que cuando se ve afectada no solo la vegetación, sino también el suelo. En este escenario, la perturbación tiene efectos de larga duración sobre la composición de las especies (Chazdon, 2003). Ejemplo de ello es el estudio de Burslem et al. (2000) que, al evaluar el efecto de la historia de uso de suelo y de cuatro huracanes en la vegetación de un bosque tropical perturbado por actividades antropogénicas, encuentra que la historia previa de uso del suelo fue la que mayormente determinó la variación en la composición de especies. Sin embargo, la combinación de la perturbación del suelo por actividades agropecuarias y un aumento en la intensidad de huracanes, podrían generar un escenario de perturbación con alteraciones a largo plazo en el BTS.

1.3 Resiliencia de los Bosques Tropicales ante disturbios naturales

La resiliencia es un término usado en diferentes áreas del conocimiento, y es un tema que se discute continuamente debido a los diferentes enfoques y definiciones que se han aplicado. En este caso se define resiliencia como la capacidad y tasa de recuperación de la estructura, composición y funcionamiento que tiene el bosque después de un disturbio. (Chazdon y Arroyo, 2013). Por otro lado, dentro de este concepto también se engloban los términos de “resistencia” y “recuperación”. El primero describe el impacto instantáneo de disturbios que se originan fuera del sistema (exógenos) en el estado del mismo. El segundo, captura los procesos que surgen dentro del sistema (endógenos) que llevan a este a un estado anterior al disturbio, al que se conoce como equilibrio (Hodgson et al., 2015). En este sentido, una evaluación en la recuperación de un sistema posterior a un disturbio, puede ser informativa para estimar el tiempo de recuperación de dicho sistema (Standish, 2014).

Para la vegetación, la frecuencia e intensidad de los disturbios puede determinar sus rangos de crecimiento, tiempo de reproducción o longevidad y, por ello, los cambios en estos factores (frecuencia e intensidad) pueden alterar su composición y estructura. En el caso de los huracanes, el grado de daño que infligen a la vegetación está definido por la intensidad de los vientos y las lluvias (Sánchez-Sánchez e Islebe, 1999). En los bosques tropicales secos en particular, los daños de estos fenómenos naturales a la vegetación, tienden a estar sesgados hacia los árboles de mayor altura y diámetro (Van Bloem et al., 2006, Vandecar et al., 2011), que son los más vulnerables a sufrir inestabilidad mecánica debido a los efectos combinados de su propio peso y la fuerza de los vientos huracanados (Fournier et al., 2006).

Por otra parte, el proceso de recuperación de la vegetación del bosque tropical seco a un disturbio de esta naturaleza, depende en gran medida de la reproducción vegetativa (rebrote). Otra contribución importante viene de la alta proporción de especies anemocóricas cuyas semillas pueden colonizar los sitios perturbados (Vieira y Scariot, 2006). En los bosques tropicales secos del Caribe, por ejemplo, la proporción de tallos con rebrotes fue de 5 a 10 veces mayor tras el paso del huracán Hugo en 1989, y aún los tallos no dañados incrementaron su producción de rebrotes como respuesta a los vientos intensos (Van Bloem et al., 2006, 2007).

En cuanto a los disturbios antrópicos, de acuerdo a un meta-análisis sobre la resiliencia en los BTS ante este tipo de disturbios (Derroire et al., 2016), puede haber una recuperación en la riqueza de especies de árboles y arbustos en los bosques secundarios, mismos que tendrían potencial para la conservación de biodiversidad a largo plazo, aunque no necesariamente llegarían a ser iguales en composición a los bosques conservados. En los bosques conservados, por el contrario, los autores observaron que la recuperación era lenta e incierta.

En este trabajo evaluaremos tanto el tipo de daño causado a la vegetación por un huracán, como la capacidad de rebrote de dicha vegetación tras este evento, en un bosque tropical seco que ha sido perturbado por actividades humanas y por un huracán de alta intensidad. Asimismo, evaluaremos si existe una relación entre el daño sufrido y la capacidad de rebrote de las diferentes especies, con atributos funcionales foliares relacionados con procesos fisiológicos fundamentales de la vegetación (v. gr. tasa de crecimiento, fotosíntesis). Esto con el fin de dilucidar las bases funcionales tanto del daño como la capacidad de recuperación, y con ello poder generar hipótesis sobre la respuesta de este tipo de vegetación al efecto sinérgico de la perturbación antrópica y el incremento potencial en la frecuencia/intensidad de huracanes.

1.4 Atributos funcionales de la vegetación del Bosque Tropical Seco.

Los atributos funcionales son características morfológicas, bioquímicas, estructurales, fenológicas o de comportamiento, que son considerados relevantes en la respuesta de algunos organismos al ambiente (Díaz et al., 2013; Chaturvedi et al., 2011). Tradicionalmente, las especies de plantas se agrupan en tipos o grupos funcionales definidos por sus funciones fisiológicas, ecológicas e historia evolutiva común (Chaturvedi et al., 2011).

Algunos atributos funcionales característicos de la vegetación del bosque tropical seco son la pérdida estacional de las hojas en respuesta a la sequía, una alta capacidad de reproducción vegetativa y la presencia de espinas, entre muchos otros (Singh y Singh, 1992, Cornelissen et al., 2003). Algunos estudios han evaluado previamente atributos funcionales foliares de la vegetación a lo largo de la sucesión secundaria del BTS (Alvarez-Añorve et al., 2012), encontrando diferencias significativas en cuanto a fotosíntesis neta, tasa de transpiración y área foliar específica, entre los sitios de sucesión temprana y los sitios de sucesión avanzada. Específicamente, los atributos funcionales variaron desde aquellos que maximizan la disipación de calor en la sucesión temprana, hasta aquellos que favorecen la adquisición de luz y el uso eficiente del agua en los estadios de sucesión tardía. Estas diferencias se relacionaron principalmente con las distintas condiciones ambientales que caracterizaban a los estadios sucesionales.

Entre los atributos funcionales que, de acuerdo a Alvarez Añorve et al. (2012), pueden ser útiles para estudiar la respuesta de la vegetación a la perturbación en los bosques tropicales secos, se encuentran: el contenido de clorofila (como un proxy de la actividad fotosintética), el área foliar específica (área foliar por unidad de peso seco), la densidad foliar (peso seco de la hoja/(área foliar * grosor) y la masa fresca por unidad de área foliar. En este estudio evaluaremos dichos atributos, así como su relación con el daño estructural sufrido por la vegetación a causa de un huracán y con la capacidad de rebrote posterior al mismo. De existir esta relación, conociendo podríamos vislumbrar su posible respuesta a huracanes de alta intensidad, así como a un aumento en la frecuencia de los mismos.

ANTECEDENTES

1.5 Estudios de la respuesta de los bosques tropicales secos a huracanes

El impacto provocado por los huracanes en sistemas de bosque seco depende de la intensidad del evento (v.gr velocidad del viento y precipitación). De acuerdo a Navarro-Martínez et al. (2012), los fenómenos que alcanzan categoría 4 o 5 en la escala de Saffir-Simpson (categorías de 1 a 5) pueden derribar hasta 33% de las ramas, mientras que los de menor categoría sólo llegan a defoliar parcialmente el dosel. Para estos autores, la recuperación del bosque puede estar dada en el siguiente orden: 1) recuperación de la fenología arbórea, 2) aumento en la producción de hojarasca e incremento en el crecimiento de las ramas, y 3) rebrote de ramas. A pesar de ser fuertemente impactados, muchos de los BTS que han experimentado este fenómeno han mostrado una notoria capacidad de recuperación.

Entre los estudios que evalúan el impacto de los huracanes en la composición florística y estructura de los bosques tropicales, la mayoría se han llevado a cabo en bosques conservados (fragmentados y/o continuos) y solo unos pocos estudios han abordado también los bosques secundarios (Sánchez-Sánchez e Islebe. 1999; Whigham et al.. 2003; Rossi et al.. 2007; Imbert y Portecop, 2008; Laurance y Curran, 2008; Vandecar et al., 2011; Lewis y Bannar-Martin, 2012; McGgroddy et al., 2013; Carrington et al., 2015).

Los principales lugares en donde se han realizado evaluaciones sobre el impacto de los huracanes en Bosques Tropicales Secos son: la península de Yucatán (Sanchez-Sanchez e Islebe, 1999; Imbert y Portecop, 2008; Bonilla-Moheno, 2010; Vandecar et al., 2011;

Rojas-Sandoval, 2014; Valdez-Hernández, 2014;), Puerto Rico (Van Bloem, 2005; Walker, 1991), y otras islas del Caribe (Van Bloem y Murphy, 2005; Imbert y Portecop, 2008).

De manera general, en lo referente a la alteración en la composición de especies, varios de estos estudios encuentran que esta no es grandemente afectada por los huracanes ya que, en la mayoría de los casos, la mortalidad de especies es relativamente baja (Van Bloem, 2005; Whigham, 1991). A ello se aúna una producción inmediata de rebrotes, lo que aminora el recambio en la composición específica.

En cuanto a los atributos estructurales, al parecer la altura y diámetro a la altura del pecho pueden determinar el tipo de daño que sufren los árboles. McGrody (2013) y Vandecar (2011), por ejemplo, encuentran que los sitios que sufrieron menor daño fueron aquellos en los que la vegetación presentaba menor altura (>10m), mientras que los árboles más altos y con mayor diámetro a la altura del pecho fueron los más propensos a sufrir algún daño. Estos árboles fueron desenraizados por el huracán en mayor proporción que los de otras categorías de tamaño (Walker, 1991). Sin embargo, la altura promedio pudiera no siempre estar relacionada con el nivel de daño sufrido (véase Imbert y Portecop, 2008).

El tipo de daño causado por el huracán, parece también estar relacionado con la capacidad de rebrote y por tanto con la recuperación de la vegetación en los bosques tropicales secos. Por ejemplo, la cantidad de rebrotes ha mostrado ser mayor en individuos desenraizados, en comparación con individuos que permanecieron arraigados (Walker, 1991), así como en troncos que sufrieron defoliación causada por los fuertes vientos, en comparación con los troncos que no estuvieron expuestos a este tipo de vientos (Van Bloem et al., 2006). Una recuperación rápida de los bosques afectados se podría deber también a la rápida recuperación de hojas, como se ha reportado en algunos estudios (Bonilla-Moheno, 2010; Brokaw and Walker, 1991).

El uso de atributos funcionales foliares para inferir simultáneamente tanto el nivel de daño como la capacidad de rebrote de la vegetación tropical después de un huracán, no se ha evaluado hasta el momento y, por tanto, no conocemos una aproximación que combine información de tipo florística, estructural y funcional, para caracterizar de forma más precisa el efecto de los huracanes de alta intensidad en la vegetación tropical. En el mismo sentido, tampoco se ha intentado detectar los atributos funcionales más útiles para predecir la respuesta de la vegetación a este tipo de fenómenos naturales y a su incremento.

1.5 Huracanes de alta intensidad en la costa del Pacífico Jaliscience

Durante el 2015, en el Océano Pacífico se presentaron trece huracanes y seis tormentas tropicales. Los primeros 8 huracanes (Andrés, Blanca, Dolores, Jimena, Linda, Olaf, Patricia y Sandra) alcanzaron un nivel de intensidad alto puesto que rebasaron los 178 km/h de velocidad del viento (Bravo, 2015). En específico, el huracán Patricia tocó tierra un 23 de Octubre en las inmediaciones de las bahías de Tenacatita, Cuastecomate y Barra de Navidad, donde se encuentran las poblaciones de Cuixmala, El Estrecho, La Manzanilla y Melaque (municipios de La Huerta y Cihuatlán, Jalisco). Este huracán se destacó por ser rápido e intenso, al pasar de categoría 1 a 5 en la escala de Saffir-Simpson en 15 horas aproximadamente, alcanzando vientos máximos sostenidos de 325 km/h. De acuerdo a la clasificación de los daños materiales, hecho por la Comisión Nacional del Agua, el nivel 5 alcanza: árboles pequeños caídos, desprendimiento de árboles, daños al tendido eléctrico, daños severos en puertas y ventanas, grietas en construcciones, fallo total en residencias y construcciones industriales (Bravo, 2015). El último huracán que impactó fuertemente en la región de Chamela fue Jova, ocurrido en octubre de 2011, mismo que llegó a ser categoría 3 en la escala de Saffir-Simpson. Este tocó tierra al Suroeste de Manzanillo, Colima, avanzando por la región de la costa de Jalisco, donde alcanzó vientos máximos sostenidos de 100 km/h, con rachas de 120 km/h (Bravo, 2011).

1.6 Justificación y características del estudio.

Por todo lo anteriormente mencionado, la región del pacífico jaliscience es un modelo ideal de estudio para evaluar los efectos del aumento en la intensidad de huracanes en la vegetación tropical, ya que la cobertura vegetal está dominada por un BTS altamente diverso, mismo que está inmerso en un paisaje antropogénico compuesto por bosques conservados (Reserva de la biósfera Chamela-Cuixmala), bosques secundarios y zonas agropecuarias. Las características de esta región nos permite comparar el efecto de estos fenómentos tanto en bosques conservados como en bosques previamente impactados por la actividad humana (bosques secundarios) y, nos permite entonces conocer si el grado de susceptibilidad de la vegetación difiere entre bosques perturbados y conservados.

Adicionalmente, dado que el evaluar simultáneamente diferentes tipos de atributos nos brinda información más precisa sobre el daño causado por el huracán, sobre la capacidad de regeneración de la vegetación, y sobre los determinantes de ambos parámetros, en este estudio evaluamos, antes y después del huracán Patricia, la composición específica de la vegetación (atributos florísticos), sus atributos estructurales (área basal, altura, número de ramas) y sus atributos funcionales foliares (contenido de clorofila, grosor, área foliar específica, masa fresca foliar). Posteriormente al paso del huracán se evaluó también el tipo y nivel de daño sufrido por la vegetación (*sensu*

Vandecar et al., 2011; Navarro-Martínez et al., 2012) y su capacidad de rebrote (número y área basal de los rebrotes) como un *proxi* de la capacidad de regeneración.

Estos atributos se evaluaron en 3732 individuos de 279 especies arbóreas, tanto en bosques secundarios como en bosques conservados de la región. Con estos datos pudimos conocer los cambios provocados por el huracán en los atributos evaluados, así como en qué medida dichos atributos se relacionan o explican el nivel de daño sufrido y la capacidad de rebrote de las diferentes especies presentes tanto en bosques conservados como en bosques secundarios de la región. Esta relación, a su vez, nos brindó información sobre las bases funcionales de la respuesta de la vegetación y puede ser útil para predecir como cambiarán los atributos de este paisaje de BTS ante un aumento en la frecuencia de este tipo de huracanes. El estudio, cuyos objetivos son los que se listan a continuación, se describe a detalle en el capítulo 2.

OBJETIVOS

Objetivo general

Comparar la vegetación de los bosques conservados y secundarios del bosque tropical seco, en términos del nivel de daño sufrido por un huracán de alta intensidad y su capacidad de recuperación, así como identificar parámetros (asociados a la composición, estructura y función) que pudieran estar relacionados tanto con el daño sufrido como con la capacidad de recuperación de dicha vegetación.

Objetivos específicos

1. Caracterizar la composición específica de la comunidad arbórea para cada tipo de bosque (conservado y secundario).
2. Caracterizar estructuralmente la vegetación arbórea y comparar, entre ambos bosques, el tipo de daño estructural causado por el huracán.
3. Evaluar la capacidad de rebrote para cada individuo arbóreo y comparar la capacidad de recuperación de la vegetación entre los bosques conservados y secundarios.
4. Identificar atributos relacionados con la composición específica, con la estructura y con la función de la vegetación, que pudieran estar relacionados al tipo de daño sufrido y a su capacidad de rebrote.

CAPÍTULO II

Structural and Functional Traits Predict Short Term Response of Tropical Dry Forests to High Intensity Hurricanes

(Artículo sometido a la revista *Forest Ecology and Management*)

Structural and Functional Traits Predict Short Term Response of Tropical Dry Forests to High Intensity Hurricanes

Authors and Affiliations

Diana Laura Jimenez-Rodríguez[a]

Mariana Yolotl Alvarez-Añorve[a]

Marisela Pineda-Cortes[b]

Jose Israel Flores-Puerto[a]

Julieta Benítez-Malvido[c]

Ken Oyama[a]

Luis Daniel Avila-Cabadilla[a]

[a]Escuela Nacional de Estudios Superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán, México. Antigua Carretera a Pátzcuaro No.8701 Col. Ex Hacienda de Sán José de la Huerta. C.P. 58190, Morelia, Michoacán, México.

[b]Instituto de Investigaciones sobre los Recursos Naturales, Universidad Michoacana de San Nicolás de Hidalgo. Av. San Juanito Itzicuaro s/n, Col. Nueva Esperanza, C.P. 58330 Morelia, Michoacán, Mexico.

[c]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, México. Antigua Carretera a Pátzcuaro No.8701 Col. Ex Hacienda de Sán José de la Huerta. C.P. 58190, Morelia, Michoacán, México.

Corresponding author:

mariana_alvarez@enesmorelia.unam.mx and luis_avila@enesmorelia.unam.mx; +52 (443) 6893500 ext. 80562. Antigua Carretera a Patzcuaro No. 8701, Expropiación Petrolera INDECO, C.P. 58190, Morelia, Michoacán de Ocampo, México.

Abstract

Tropical dry forest (TDF) is the most threatened of all tropical forest ecosystems worldwide. In the tropical dry forest of the Pacific Coast of Mexico, in addition to human disturbance, the vegetation has been subjected to natural disturbances such as droughts and hurricanes. The average cyclone intensity and the number of very intense category 4 and 5 storms are predicted to increase in this area and such extreme meteorological events generate further stress to the vegetation. Given that in October 2015 the category 4 hurricane “Patricia” landed on the Chamela-Cuixmala TDF, in this study we: (1) evaluated the effect of high intensity hurricanes on TDF vegetation at two habitat types (secondary forest vs old-growth forest); and (2) determined how the vegetation attributes at the species and stand level could be defining the vegetation type of damage, and its recovery capacity. For this purpose we evaluated species composition, vegetation structure and individuals biomechanical traits in eight vegetation plots, four corresponding to old-growth forests (OGF) and four corresponding to secondary forests (SF), before and after the hurricane. Additionally, after the hurricane we also evaluated the damage, leaf functional traits and resprouting ability at the individual level. In total we evaluated 3732 individuals of 279 species. Data were analysed by contrasting the vegetation damage and recovery capacity (re-sprouts) between SF and OGF. Then, we evaluated for the potential relationship between vegetation composition and structure (stand-level attributes) and vegetation damage and recovery capacity. Finally, we evaluated the association between biomechanical and leaf functional traits and the vegetation damage and recovery at the species/individual level. In general, we found that OGF received a greater proportion of damage and it could show a lower proportion of species with high resprouting capacity than SF. Most severe types of damage were biased toward stems of larger diameter and toward taller trees as they could be more vulnerable to mechanical instability. On the other hand, stems taller and with larger diameter were included among the individuals producing the lowest number of resproutings. Resprouting ability was also associated to leaf functional traits such as chlorophyll content and leaf density indicating a greater biomass acquisition in species with higher photosynthetic capacity. These results suggest that in scenarios of increasing frequency and/or intensity of hurricanes, the TDF of the Pacific Coast of Mexico could change their physiognomy toward a canopy of lower height with trees of lower diameter in average. The proportion of species with strategies resistant to damage and favoring recovery (i.e smaller sizes, productive and resistant tissues) could increase as well.

Key words: Hurricanes; Vegetation structure; Leaf functional traits; Biomechanics traits; Resprouting; Secondary forest; Tropical dry forest

1. Introduction

Tropical dry forest is the most threatened of all tropical forest ecosystems worldwide (Miles et al. 2006). Contemporary changes of land use and cover in neotropical dry forests (e.g., fragmentation and deforestation) have lead to complex landscapes in which patches of old-growth forests, secondary forests, cattle ranging areas and agricultural uses co-occur (Chazdon et al., 2009; Sánchez-Azofeifa et al., 2009). More recently, global climatic change is considered as an emerging threat for the persistance and functioning of dry tropical ecosystems (Murray-Tortarolo et al. 2016). Natural and human-induced disturbances shape forest systems by influencing their composition, structure and functional process (Dale et al, 2001). Each disturbance type affects forests differently. Some cause large-scale tree mortality, whereas other affect community structure and organization without causing massive mortality (Dale et al, 2001). Generally, plant community structure, diversity, composition, functional traits and phylogenetic structure differ among secondary forests of different ages and between old-growth and secondary forests (Poorter et al. 2004).

In the tropical dry forest of the Pacific Coast of Mexico, the Chamela-Cuixmala Biosphere Reserve, in addition to human disturbance, the vegetation has been subjected to natural disturbances such as droughts and hurricanes. These extreme meteorological events generate further stress to the vegetation (Lugo et al., 2010). The effects of hurricanes on vegetation include sudden and massive tree mortality, complex patterns of tree mortality and altered patterns of forest regeneration (Lugo et al. 2002, Dale et al. 2001). Furthermore, in species-rich tree communities with high levels of endemisms and species turnover such as tropical dry forests, vulnerability to extinction after a major disturbance is taxonomically dependent (Vamosi and Wilson 2008, Santos et al. 2010). Empirical information, however, regarding the impact of hurricanes on the diversity, structure and composition of tree assemblages in old-growth forest and secondary tropical dry forest landscapes is incomplete or missing. So far, there is evidence that tree communities in secondary forests are structured by a few phylogenetically closely related families, whereas old-growth forest tree communities are dominated by late-successional species from many distant families (Kelly et al., 2008; Álvarez-Añorve et al., 2012). Furthermore, the functional composition of the tree community changes with forest succession (Lohbeck et al. 2013).

Over a four-year period hurricanes have landed twice in the Pacific Coast of Mexico, directly impacting the area where the Chamela-Cuixmala Biosphere Reserve is located: category 2 Hurricane Jova, in October 2011, and category 4 Hurricane Patricia, in October 2015. This is in agreement with studies indicating an increase in average cyclone intensity and the number of very intense category 4 and 5 storms in the Pacific coast of Mexico (Knutson et al. 2015). These extreme meteorological events produced major changes in several aspects of ecosystem functioning including rainfall and runoff dynamics and primary productivity (M. Maass et al. this number).

In the present study, we tested whether or not the level and type of damage (in stems and tree crowns) inflicted to the standing vegetation by Hurricane Patricia (strong winds and rainfall), is influenced by the previous anthropogenic disturbance of the dry forest (i.e., old-growth forest and secondary forest). Since early-successional species tend to dominate in secondary forests, we hypothesized that the magnitude of hurricane damage to the vegetation would differ from old-growth forests as early successional species represent different life histories and regeneration strategies as well as distinct funtional traits (e.g., stem density). Besides, the anthropoghenic and natural disturbances interact influencing the severity of the perturbation as well as the rate of recovery in tropical forests (Chazdon 2003). Secondly, we tested the hypothesis that there is a significant relationship between vegetation structural and functional traits (at the stand level and at the individual level) and their preponderant type of damage and recovery capacity. The existence of this relationship would allow us to identify predictors of the impact and response to high intensity hurricanes by TDF vegetation. The main goals of this study were: (1) to evaluate the effect of hurricanes on tropical dry forest vegetation at two habitat types (secondary forest and old-growth forest); and (2) to determine how the vegetation attributes at the species and stand level could be defining the vegetation type of damage, and its recovery capacity. For this, we first contrasted the vegetation damage and recovery capacity (re-sprouts) between secondary forests and old-growth forests. Then, we evaluated for the potential relationship between vegetation composition and structure (stand-level attributes) and vegetation damage and recovery capacity. Finally, we evaluated the association between biomechanical and leaf functional traits and the vegetation damage and recovery at the species/individual level.

2. Materials and Methods

2.1. Study region and sampling sites

This study was carried out in and around the Chamela Cuixmala Biosphere Reserve (CCBR; 19º22’-19º35’N, 104º56’-105º03’W), in the pacific coast of Mexico, where a marked seasonal fluctuation in the precipitation regime occurs (www.ibiologia.unam.mx/ebchamela/www/clima.html). In this area, the average annual precipation is 915 ± 311 (SD) mm (data for the last two decades), and the dry season lasts approximately seven months, from November to May (García-Oliva et al. 2002, Chamela Biological Station 2017). Because of the prevalence of these climatic conditions, the main vegetation covers in this area include the TDF and the riparian forest (Lott et al. 2002). Nevertheless, the accelerated increase in human activities, mostly due to agriculture and cattle ranching, has caused a significant decrease in these vegetation covers. That's why the actual remaining coverage of TDF reaches the 56.1%, whereas the remaining coverage of the riparian forest reaches the 3.7% (Sanchez-Azofeifa et al. 2009).

The set of permanent plots used for this study was established and sampled before the arrival of the hurricane Patricia. These sites have been used as part of a project looking to evaluate the use of spectral reflectance of the vegetation for the study of functionality and diversity of tropical plants communities (CONACyT CB-222202). In total, we used for this study eight sampling sites representing two habitat types (four old-growth forests and four secondary forests sites), which were selected with the help of Google Earth high-resolution imagery (http://earth.google.com), classified satellite images, and the information provided by landowners and farmers (Avila-Cabadilla et al. 2012, Fraga et al. 2017). Each site was defined by a plot with an area of 1000 m^2 (50 x 20 m) and separated each other by a distance ranging 1 to 32 km (Fig. 1). Coincidentally, all sampling sites were located in the same area of influence of the hurricane Patricia (area of maximum influence), where the sustained winds averaged 119 km/h and the gust reached 241 km/h (Kimberlain et al. 2016).

Patricia was a late-season hurricane that reached the category 5 (on the Saffir-Simpson Hurricane Wind Scale), due to the anomalously warm waters present in the south of Mexico. This hurricane, considered up today one of the strongest registered in both, the easter North Pacific and North Atlantic basins, reached a peak intensity of 333 km/h and a minimum central pressure of around 879 hPa. Nevertheless, this hurricane weakened substancially –became a category 4 hurricane– before making landfall (2300 UTC, 23 October 2015, end of the rainy season) near Cuixmala beach, lowering its intensity to 241 km/h (minimum central pressure of 932 hPa).

2.2. Vegetation sampling

On each sampling plot we identified and georeferenced, with the help of a MobileMapper 20 (Spectra Precision, 50 cm error after the post-processing differential correction), all woody plants with a diameter at breast height (DBH; 1.30 m) equal or greater than 2.5 cm. For each individual, we recorded the following information: 1) the species, 2) the number of all branches at 1.30 m, 3) the DBH, and 4) the height. Additionaly, we estimated the leaf area index (LAI) in 30 points, regurlarly distributed every 5 m, along three 50 m transects. For this purpose we recorded, at each point, three measurements toward each cardinal point (twelve measurements in total), performing a reference reading every 30 min in an open space, in order to correct for sunlight brightness variations. The LAI is the area occupied by the vegetation after projected in a horizontal plane, and clearly reflects the variation in the number of strata (Fournier et al. 2003). All LAI measurements were carried out during the morning (from 09:00 to 11:00 h), with the LAI-2000 Plant Canopy Analyzer (LI-COR, USA), always using a viewcap of 45º.

At the end, we estimated the following parameters characterizing the vegetation structure at the stand level: 1) the total number of individuals, 2) the total number of branches, 3) the stand basal area, 4) the average heigh of the 30 highest individuals (emerging trees), 5) the average LAI, 6) the average nearest neighbor distance and 7) the density, which is the average density of points (individuals). The last two metrics characterize the spatial patterns of vegetation, which could be also modulating its response to hurricanes, and were estimated with the "spatstat" package for the R software (Baddeley et al 2016). The taxonomic designation of species follows "The Plant List" (http://www.theplantlist.org).

2.3. Hurricane damage and vegetation recovery

During the six months after the landfall of the hurricane Patricia, we assessed the damage caused to the vegetation by assigning individuals to one of the eight categories of damage previously used by Navarro-Martínez et al. (2012). The lack of leaves in the plants because of the dry season and the hurricane winds facilitated the evaluation of the vegetation damage. Specifically, we assigned individuals to one of the following categories (from a high to a low level of damage): 1) dead tree, 2) uprooted tree, 3) broken trunk, 4) bent trunk, 5) inclined trunk, 6) tree without branches, 7) secondary broken branches, and 8) undamaged tree (Fig. 2).

Additionaly, we evaluated the short term resprouting capacity of each individual by estimating: 1) the number of resprouts, and 2) the total basal area of resprouts. This evaluation was carried out at the end of the growing season (September-October 2016) following the hurricane landfall.

2.4. Plant functional traits

For this study, we considered a set of fundamental leaf functional traits that (a) strongly influence plant growth and survival, (b) properly reflect plant response to changes on the environmental conditions and resources availability, and (c) have been successfully used for elucidating the mechanisms underlying the vegetation response to several types of disturbance in TDF (Alvarez-Añorve et al. 2012). Specifically, we estimated the following traits: chlorophyll content (CC), measured with a SPAD-502Plus Meter (Konica Minolta Sensing Europe); specific leaf area (SLA, leaf area per dry mass); leaf density (LD, leaf dry mass / (leaf area x leaf thickness); and the leaf fresh mass per unit area (LFM). For the estimation of leaf parameters we collected, in each sampling plot, 5 fully expanded, sun exposed, mature leaves per individual, without herbivores damage. The leaves collection and measurement were conducted during the rainy season – when most plants presented leaves – following standard methods (Pérez-Harguindeguy et al. 2013). Collected leaves were immediately placed in sealed plastic bags containing moistened paper towels and transported to the laboratory in a cooler for the measurement of weight, thickness, and area. Leaf area was determined by analyzing leaf photographies (maintaining a fixed distance from the camera of 50 cm) with the ImageJ software (https://imagej.nih.gov/ij/) or by using the LI-3000C portable area meter (1 mm^2 resolution, LI-COR, USA), coupled with the LI-3050C transparent belt. The processed leaves were then oven dried for 72 h at 70ºC and weighed again to determine dry mass.

The leaf functional traits were determined at the end of the growing season following the hurricane landfall for those species grouping at least the 80% of sampled individuals, following the suggestion of Cornelissen et al. (2003). We focused on these species because they provide enough information to scale-up the traits values to the community level and they have the highest impact on the ecosystem processes.

We also estimated the values corresponding to whole plant traits: DBH, height (describe above), and wood density (WD). These biomechanical traits were selected because of their contribution to the risk of mechanical instability in trees as they involve the characteristics of pole size (height, diameter) and weight (wood density) (Fournier et al. 2006). Besides, wood density provides a good predictor of the impact and response to cyclones by individual tree species (Laurance and Curran 2008). Wood density values were obtained from published databases (Kattge et al. 2011, Paine et al. 2015).

2.5. Data analysis

We used non-Metric Multidimensional Scaling (MDS) ordinations for mapping the variation among plant communities in terms of species composition – based on Bray-Curtis dissimilarity matrices –, and vegetation structure – based on Euclidian distance matrices (McCune and Grace 2002). For the species composition ordination, we used the square root of the number of individuals to avoids biases toward the species with the largest difference in abundance (Kindt and Coe 2005), whereas for the ordination regarding vegetation structure, we normalized to a 0 – 1 range all the variables (vegetation attributes) to avoid the effect of differences on their scale of measurement. At the end, we used the stress value, scaled from 0 – 100, to evaluate how successfully the resulting ordination reflects the distance between communities in the original dissimilarity matrices (lower values indicate more reliable ordinations). Finally, we used the "envfit" analysis to test for potential significant effects of habitat on community composition, vegetation structure and type of damage. This function estimates the centroids corresponding to each habitat type in the resulting ordination spaces and then evaluates if the observed distance among centroids is greater than expected by chance. The significance testing ($P \leq 0.05$) was always based on 10000 permutations. The analyses were carried out with the help of the “vegan” R package (Oksanen et al 2015).

2.6.1. Damage and vegetation recovery in secondary and old growth forests

First, we explored the distribution of individuals (frequency) across the different categories of damage and across different levels of resprouting capacity, by mean of histograms separately built for each habitat type. In addition, we related the distribution of individuals in each category with their height and basal area.

Second, we used non-Metric Multidimensional Scaling (MDS) ordinations for mapping the variation among plant communities in terms of vegetation damage – based on Euclidian distance matrices – (McCune and Grace 2002). For this ordination, we standardized the abundance data by dividing the abundance of each cell (number of individuals corresponding to each category of damage) by the total number of sampled individuals. The “envfit” analysis (described above) was also used to test for significant differences between habitats.

Third, we used the generalized linear models (GLMs) to evaluate for the potential effect of the type of habitat on the number of individuals presenting every type of damage, as well as on the resprouting capacity: individual mean number of resproutings and resprouting basal area. The number of individuals and the number of resprouts were modeled with the Poisson distribution and the “log link” function, whereas the total basal area of resproutings was modeled with the Gaussian distribution and the “identity link” function. The analyses were carried out using the R software (R Core Team 2016).

2.6.2. Relationship between vegetation structure and composition with vegetation damage and recovery

First, we evaluated the potential associations between the vegetation damage and its species composition and structure by comparing the corresponding ordinations (explained above) via the “Procrustes” and “Protest” analyzes. This allowed us to rotate the configuration resulting from these ordinations to reach their maximum similarity, and then test for the significant association between such configurations with a correlation like statistic. The significance ($P \leq 0.05$) of the statistic was evaluated also through a randomization test (10000 permutations). The analyses were carried out with the help of the “vegan” R package (Oksanen et al 2015).

Second, we used GLMs to model the variation in the number of individuals corresponding to each category of damage, and to resprouting capacities (individual mean number of resproutings and resprouting basal area), with respect to the variation in plant species composition and vegetation structure. For this purpose, we considered as explanatory variables the sampling sites scores from ordinations regarding species composition and vegetation structure, which can be considered as continuous synthetic variables summarizing the variation among plant communities in relation to these attributes. The response variables were modeled considering the distribution and link function mentioned above. The best set of predictors – the ones included in the sets of most plausible models – were detected by performing model selection based on the estimation of the small-corrected form of the Akaike's information criterion (AIC_c, Burnham and Anderson 2002). We estimated, for the entire set of potentials models, the AIC_c, the delta AIC (ΔAIC, AIC differences between each model and the best one), and the AIC weights (W_i), which represents the weight of evidence that a given model is the best model among the set of candidate models. The set of most plausible models included all models for which: 1) the ΔAIC_c was lower than 2, and 2) the sequential sum of W_i reached 0.95 (Burnham and Anderson 2002). We also corroborated if the selected predictors presented a significant P-value ($P \leq 0.05$). The R squared (R^2) – for models with Gaussian distribution–, and percentage of deviance explained with respect to the global model – for models with Poisson distribution –, were used to evaluate the goodness-of-fit of the selected set of models. The analyses were carried out with the help of the "glmulti" R package (Calcagno 2010).

2.6.3. Relationship between plant functional traits and species damage and recovery

Finally, we tested the hypothesis that there is a significant relationship between species functional traits and their type of damage and resprouting capacity, by using phylogenetic independent contrasts (PIC, Felsenstein 1985, Garland, Harvey and Ives 1992). The PIC allowed us to account for the degree to which species are related and hence their corresponding information do not represent independent data on the analyses – phylogenetic autocorrelation. For this analysis, we used the methods provided by the "caper" R package: 1) the crunch function for the calculation of PICs for continuous variables, and 2) the brunch function for the calculation of PICs for categorical variables (Orme et al. 2012). Both functions start by calculating phylogenetically independent constrasts in a set of variables and then perform linear models of those contrasts to test for the hypotheses. We considered as response variables the number and basal area of resproutings – continuous variables – and the preponderant type of damage – categorical variables –. We analyzed for the potential drivers of every type of damage by contrasting the species that presented the corresponding type of damage *versus* the ones that did not present such type of damage (dichotomous response variables). We built linear models by considering the additive effect of two sets of predictors (traits): (1) leaf traits, CC + LD + LFM + SLA; and (2) whole-plant traits, DBH + WD + Height; allowing us to identify which predictors best explained the variation on the response variable. All contrasts model functions enforce regression through the origin (Garland et al. 1992).

The phylogenetic tree representing the evolutionary relationship among all taxa included in the analyses was built using as backbone the megaphylogeny generated by Zanne et al. (2014) and updated by Qian and Jin (2016). This megaphylogeny can be considered the largest and most up-to-date, time-calibrated, species-level phylogeny of seed plants. From this megaphylogeny, we generated an ultrametric tree with branch lengths in units of time (millions of years) (Fig. S1).

3. Results

In old growth forests, the most speciose family was Euphorbiaceae with 12 species (4.3 % of all species) and the most dominant species were: *Apoplanesia paniculata, Bonellia nervosa, Caesalpinia eriostachys, C. platyloba, C. pulcherrima, Celosia monosperma, Cordia eleagnoides, Croton roxanae, C. suberosus* and *Guapira macrocarpa*. In addition, the vegetation in these plots presented an average species number of 55 (range: 45 – 62), and an average individuals number of 631 (range: 508 – 705). In constrast, in the SF plots the most speciose family was Leguminosae with 25 species (9.0 % of all species), whereas the most dominant species were: *Acacia cochliacantha, Bauhinia ungulate, Caesalpinia coriaria, Casearia corymbosa, Coccoloba liebmannii, Cordia alliodora, Croton alamosanus, Eugenia capuli, Guazuma ulmifolia* and *Haematoxylum brasiletto*. These vegetation plots presented an average species number of 48 (range: 20 – 76), and an average individuals number of 444 (range: 248 – 638). These differences between the plant communities associated to both types of habitat were also evident in the ordination space (Fig. 3A), where a significant segregation of the two types of plant communities was observed ("envfit" test, $r^2 = 0.56$; $P = 0.03$).

We also found significant differences ("envfit" test, $r^2 = 0.42$; $P = 0.03$) between OGF and SF plant communities regarding vegetation structure (Fig. 3B). The OGF presented a more complex structure, characterized by a higher number of individuals, number of branches, stand basal area, height, leaf area index (number of strata) and density of individuals, as well as by a lower average nearest neighbor distance among individuals. The average height of the tallest trees in this forest (considering the 30 emergents) was 9.14 m (range: 8.42 – 10.18 m), whereas the average height of the tallest trees in SF was 5.96 m (range: 4.75 – 7.27 m).

3.1. Damage and vegetation recovery in secondary and old growth forests

In general, we sampled and characterized the damage and resprouting capacity of 3734 individuals (1591 for SF and 2143 for OGF), comprising 279 species and morphospecies. This allowed us to identify that both types of habitat suffered significant damage (Fig. 4) – most of their individuals were damaged – and that the most common type of damage in both habitats was "inclined trunk", followed by "bent trunk" in OGF and by "secondary broken branches" in SF (Fig. 5A). On one hand, we found that OGF vegetation was the most affected by the hurricane, presenting the highest percentage of dead trees (8.46%). Here, almost the 24.28% of individuals presented one of the three most severe types of damage ("dead tree", "uprooted tree", and "broken trunk"). On the other hand, the SF vegetation was less affected, showing the highest percentage of undamaged trees (11.01%) and a lower percentage of individuals with the three most severe types of damage (9.89%). The same pattern arises when we test for the potential effect of the type of habitat on the number of individuals presenting different types of damage (Table 1). For example, we detected that most individuals corresponding to the categories "dead tree", "uprooted tree", "broken trunk", "bent trunk", "inclined trunk" and "tree without branches" were found in OGF whereas most individuals corresponding to the categories "secondary broken branches" and "undamaged trees" were found in SF. In both habitats, the tallest trees and the ones presenting the highest basal area were included among the most affected plants (Fig. 5B). Nevertheless, when we mapped the variation among plant communities in relation to the overall distribution of individuals accross the different types of damages, we did not found a significant segregation of plant communities corresponding to OGF and SF ("envfit" test, $r^2 = 0.19$; $P = 0.31$).

Regarding the resprouting capacity, we detected that the highest percentage of individuals producing a higher number of resproutings (> 30 resproutings) are found in OGF (4% of 2143 individuals for OGF *vs* 3% of 1591 individuals for SF), whereas the highest percentage of individuals producing a reduced number of resproutings (< 10 resproutings) are found in SF (52% for SF *vs* 49% for OGF) (Fig. 6A, Table 1). In addition, we found that in both, OGF and SF, the tallest trees and those with the highest basal area are included among the individuals producing the lowest number of resproutings (< 10 resproutings) (Fig. 6B). No significant differences were detected among habitats in terms of resprouts basal area.

3.2. Relationship between vegetation structure and composition with vegetation damage and recovery

The overall variation among plant assemblages in terms of vegetation damage (Fig. 3C) was neither correlated to their variation in species composition ($t_{\text{procrustes correlation}} = 0.35$, $P = 0.64$), nor to their variation in vegetation structure ($t = 0.38$, $P = 0.52$). Nevertheless, we found that a fraction of the variation in vegetation structure and species composition is significantly associated to the variation in the number of individuals showing some specific types of damage (Table 2). Regarding vegetation structure, we found that the highest number of dead trees, uprooted trees and bent trees were in areas with higher stand basal area and where the emergent trees are higher, whereas the highest number of undamaged trees occurred in the opposite conditions (Fig. 3B and C, Table 2). In addition, we found that the highest number of trees with broken and inclined trunks as well as with secondary broken branches, were associated to areas with a higher number of strata (LAI) and density of individuals, and a lower nearest neighbor distance among individuals. The variation in vegetation recovery capacity (number of resproutings) was significantly associated only to the variation in plant species composition (Table 2).

3.3. Relationship between plant functional traits with species damage and recovery

The families grouping the species with one of the most severe type of damage (“dead tree”, “uprooted tree”, and “broken trunk”) in both habitats are: Convolvulaceae, Hernandiaceae, Euphorbiaceae, and Leguminosae (the last two families are the most speciose ones) (Table

S1). Considering the species, most dead trees belong to the species *Croton suberosus* (0.42 % of the overall sampled individuals and 5.12 % of the conspecifics) and *Croton roxanae* (0.42 % and 4.80 % respectively) of the Euphorbiaceae family.

We also found that the species producing a higher number of resprouts belong to the family Moraceae (31 resproutings in average), Simaroubaceae (21 resproutings in average) and Celastraceae (12 resproutings in average), whereas those producing resprouts with a higher basal area belong to the families Polygonaceae (average basal area of 26.22 cm^2), Bignoniaceae (26.13 cm^2) and Acanthaceae (14.40 cm^2).

The analysis of the relationship among leaf traits and the species recovery capacity, performed for 122 species and 3238 individuals (44 % of the species and 87 % of the sampled individuals), reveals that the best predictors of the species recovery capacity are CC and LD (Table 3). In this sense, we found that the species producing the higher mean number of resprouts are those with a higher CC and LD (Table 3).

In the analysis regarding whole-plant traits, we considered 81 species and 2212 individuals, representing the 29% of the species and the 59.2% of all sampled individuals. These analyses showed that: 1) species corresponding to the categories “bent trunk” and “broken trunk”, presented a lower basal area, 2) species in the “broken trunk” category were the tallest ones, 3) species in the “inclined trunk” category were those with a lower wood density and height and 4) species producing resprouts with a higher basal area were those with a lower “wood density” and “height” (Table 4).

4. Discussion

To our knowledge, there is no a previous study evaluating, at the same time, the functional, resprouting and structural traits of such a high number of individuals (3734) in order to evaluate the TDF vegetation response to hurricanes (damage and recovery). This detailed evaluation encompassing 279 different species gave us a deep insight into the response of TDF vegetation to meteorological events that are increasing in frequency as a consequence of global warming.

Before the arrival of Patricia, the old growth and secondary forests were different in vegetation composition and structure, as hypothesized. The different species composition between OGF and SF, as well as a greater dominance of Legumes in SF, is expected because the members of this family exhibit several functional traits that confers them advantages in harsh environments such as those of secondary forests (Alvarez-Añorve et al. 2012). As a high proportion of legumes are N fixers, they are able to deal with the low nutrient and water availability characteristic of degraded soils, and they are favored in the colonization of disturbed sites. Besides, being functionally different from the rest, they experience a reduced competition for soil nitrogen (González-Iturbe et al. 2002). This could explain their clear dominance in secondary forests. A higher number of plants having compound leaves have been reported in other TDF early stages (Lohbeck et al. 2013, Buzzard et al. 2015). In the same sense, vegetation structural differences between both habitat types, as well as a higher structural complexity in OGF, have been previously reported (Alvarez-Añorve et al. 2012, Quesada et al. 2013).

4.1 Effect of stand-level attributes on vegetation damage and recovery capacity

According to our results, the highest percentage of dead trees as well as the greater proportion of individuals suffering the most severe types of damage were found in OGF. In general, tallest trees and the ones presenting the highest basal area were the most affected trees (Fig. 5B). These types of individuals are typically more frequent in OGF and this could explain the greater percentage of dead trees and the higher occurrence of severe types of damage in this habitat. In fact, hurricane damages in TDF vegetation tend to be biased toward stems of larger diameter (Van Bloem et al 2006) and toward taller trees (Vandecar et al. 2011) as they could be more vulnerable to mechanical instability due to effects of self-weight, wind forces or the combination of both (Fournier et al. 2006). Bending, which is one of the most frequent type of damage in this study, occurs when a force component such as strong winds, is acting perpendicular to the trunk. When bending stresses exceed the material strength, the trunk breaks (Fournier et al. 2006), as occurred frequently in OGF. In this sense, tall trees would experience a greater mechanical instability caused by strong winds and this would determine a higher probability to be bent or broken (Table 4).

In general, the stand level vegetation structure played a major role on the type and quantity of damage caused by the hurricane. For instance, the main reason explaining a higher number of damaged individuals in OGF is the “domino effect” caused by fallen trees. In OGF there is a greater vegetation structural complexity than in SF as the trees are taller, there are more woody individuals per area (higher density) and consequently a lower nearest neighbor distance among them. In this scenario, every fallen tree causes greater damage in OGF than in SF. This explains the higher number of trees with broken and inclined trunks as well as with secondary broken branches found in this habitat. Our results suggest that OGF vegetation would be more vulnerable to the increment on the frequency of high intensity hurricanes.

On the other hand, the resprouting capacity could also be lower in OGF as the stems that are taller and with larger diameter were included among the individuals producing the lowest number of resproutings. Although there are a great proportion of shrubs in the woody vegetation of this TDF, emergent (tallest) individuals are always trees, a life form with lower resprouting capacity than shrubs (Paciorek et al. 2000). The number of resproutings was influenced by species composition (Table 2) as this capacity can differ among families. Specifically, resprouting rates and mortality rates of resprouted individuals have shown significant differences among tropical families (Paciorek et al. 2000). In this study, families such as Moraceae, Simaroubaceae, Celastraceae, Polygonaceae and Bignoniaceae showed higher number of resprouts per individual or resprouts with a higher basal area.

However, while the resprouting capacity could differ among size classes or species, a great proportion of the stems (more than 50%) and species evaluated in this study produced resprouts after the hurricane. This coincides with the general patterns observed in tropical forests, where a majority of damaged saplings and trees resprout after hurricanes (Walker 1995). In Caribbean TDFs in particular, the proportion of stems with resprouts varied from 5 to 10 fold higher after the hurricane Hugo (1989), and even the undamaged stems increased their resprouts production as a response to other aspects of high winds, such as short-term gravitational displacement or sway (Van Bloem et al. 2006, 2007).

These findings confirm that resprouting ability is an important component of a species life history, and is likely to be important in forest community dynamics, particularly after severe disturbance. Resprouting, indeed, involves numerous ecological advantages associated with persistence following disturbances. While on a few years sprouts has the capacity to form a dense canopy of several meters in height (Kauffman 1991), reestablishment through seed sources can be limited by high rates of seed predation by ants and small rodents, and by physiological limitations to survival. Species with animal dispersed seeds, will also be in disadvantage as vectors will not move into large clearings (Nepstad 1989). These limitations to regeneration through seed sources could be more pervasive in open, hotter and drier sites such as secondary forests. Therefore, even when OGF could be more vulnerable to damage and could show a lower resprouting capacity than SF, regeneration through seeds could be less limited in this habitat.

4.2. Effect of species-level attributes on vegetation damage and recovery capacity

Analysis on the influence of species-level attributes on vegetation damage and recovery capacity, showed that the most severe types of damage ("dead tree", "uprooted tree", and "broken trunk") could be related to species characteristics such as biomechanical traits (i.e. wood density and height) or abundance. Species such as *Ipomoea wolcottiana* (Convolvulaceae), *Gyrocarpus jatrophifolius* (Hernandiaceae) or *Jatropha platyphylla* (Euphorbiaceae), members of the families associated to the most severe types of damage, show wood densities from intermediate to low (Table S1) and at least *I. wolcottiana* and *J. platyphylla*, tend to be emergent trees with high basal area. This combination of traits would result in a higher susceptibility to damage under strong winds and to the fall of neighbor trees. In this sense, previous studies have suggested that trees with higher wood densities are more resistant to cyclone damage than trees with lower wood densities (i.e. Franklin et al. 2004, Falster 2006, Curran et al. 2008). The negative relations between WD and the most severe types of damage (Table 4) support this hypothesis. Curran et al. (2008), for instance, report that wood density was able to explain 71.5% of the variation between species in ability to resist damage in an Australian tropical forest. Moreover, our results (Table 4) suggest that low dense stems present more probability to be inclined, bent or uprooted by strong winds.

On the other hand, species such as *C. suberosus* and *C. roxanae* (Euphorbiaceae), were the most abundant in the study system, and therefore they concentrated more dead individuals than other species. A great quantity of damage is also concentrated in the Legumes, which belong to the most abundant family in TDF (Lott and Atkinson 2002).

With respect to the influence of functional traits on the resprouting capacity, we detected that the production of a high number of resprouts as well as of resprouts with higher basal are, was concentrated in certain families represented by species such as *Ficus cotinifolia* (Moraceae), which tends to reproduce by resprouting, *Pristimera celastroides* (Celastraceae) and *Recchia mexicana* (Simaroubaceae). Other families also concentrated this (Polygonaceae and Bignoniaceae). *Ficus cotinifolia* and *P. Celastroides* present from low to intermediate wood density (0.39 and 0.58 respectively) which could be related to a high resprouting capacity, as wood density is negatively related to the production of sprouts in terms of both, number and basal area (Table 4). Species with low wood density have shown greater levels of resprouting in other studies where this trait was able to explain 92.2% of the variation between species in the rate of biomass reacquisition (Curran et al. 2008). Thus, low wood density species would experience higher rates of damage but also the greatest amount of biomass acquisition after hurricanes.

Despite the high phylogenetic conservatism of wood density, some of the families most associated to a high resprouting capacity in this study (Simaroubaceae, Celastraceae and Bignoniaceae) have shown great variability in wood density (Chave et al. 2006, Swenson and Enquist 2007). This high variability could be associated to a high plasticity in their resprouting capacity as wood density and the rate of biomass acquisition are related (Curran et al. 2008).

Resprouting ability was also associated to leaf functional traits such as chlorophyll content and leaf density. Specifically, the positive relation between the number of resprouts and the chlorophyll content, indicates a greater biomass acquisition in species with higher photosynthetic capacity. A high photosynthetic activity is positively related to high growth rates and low wood densities as well, which coincides with our previous findings. A high number of resprouts is also associated to a high leaf density, a trait positively associated to leaf thickness and negatively associated to SLA (Niinemets 2001). A high LD confers a higher mechanical stability to leaves while thoughness decrease defoliation during strong winds (Niinemets 2001, Laurance & Curran 2008). In this sense, species with high photosynthetic activity and dense/though leaves would produce a greater number of resprouts. These findings suggest that after severe disturbances such as high intensity hurricanes, the species with a combined strategy of high productive (that could be translated in fast growth rates) and resistant tissues could be favored through resprouting.

Synthesizing both, the old growth and secondary TDF, are highly vulnerable to high intensity hurricanes as most of their individuals (90% approximately) were damaged. However, the OGF received a greater proportion of damage and it could show a lower proportion of species with high resprouting capacity than SF. Even when OGF could face a lower limitation in regeneration through seed sources, probably SF could still have an advantage in regeneration through sprouting, as species with low wood density, high photosynthetic capacity and thougher leaves, which showed more resprouting capacity, are more abundant in disturbed forests (Alvarez-Añorve et al. 2012).

These results suggest that in scenarios of increasing frequency and/or intensity of hurricanes, the TDF of the Pacific Coast of Mexico could change their physiognomy toward a lower height canopy with trees of a lower diameter in average. The proportion of species with strategies resistant to damage and favoring recovery (i.e smaller sizes, productive and resistant tissues) could increase as well. A sustained regime of frequent hurricanes could even favore changes in tree architecture (i.e. greater branching), allometric relations and wood quality, that are caused by the mechanical stimulation of the aerial parts (Herrel et al. 2006). Pacific TDF could therefore turn more similar to Caribbean TDF, which are more subjected to disturbances caused by hurricanes (Van Bloem et al. 2006).

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Tables

Table 1. Comparisons between secondary and old growth forest in relation to the number of individuals corresponding to each category of damage and vegetation resprouting capacity.

Parameters	**Secondary forest mean (range)**	**Old growth forest mean (range)**	**R^2_{dev}**	**Z; P - value**
Damage				
Dead tree	32 (17 – 38)	39 (6 – 99)	0.02	***-1.78; 0.07***
Uprooted tree	11 (2 – 22)	37 (22 – 56)	0.57	**-7.12; 0**
Broken trunk	21 (17 – 25)	71 (60 – 77)	0.96	**-12.20; 0**
Bent trunk	69 (34 – 90)	112 (82 – 111)	0.42	**-6.25; 0**
Inclined trunk	174 (42 – 175)	253 (196 – 337)	0.17	**-7.58; 0**
Tree without branches	2 (0 – 4)	6 (4 – 10)	0.05	**2.34; 0.02**
Secondary broken branches	121 (75 – 178)	103 (74 – 160)	0.55	**-3.04; 0**
Undamage tree	15 (5 – 26)	11 (4 – 21)	0.09	***1.75; 0.07***
Recovery				
Number of resprouts	2863 (799 – 4814)	4805 (2961 – 6905)	0.06	**3.62; 0**
Resprout basal area	2.05 (1.69 – 2.34)	2.27 (1.96 – 2.77)	0.00	0.21; 0.84

n = 8. R^2_{dev} is the fraction of the total deviance explained by a model when the Poisson error distribution was used; R^2 is used with the normal error distribution. Significance of the P – value (< 0.05) is shown in bold, and marginal relationships (0.05 < P < 1.00) is shown in bold italic. Detailed information about these analyses are presented in the method section.

Table 2. Most plausible models explaining the relationship between vegetation damage and resprouting capacity and the vegetation structure and composition.

Parameters	**Model**	**R^2_{dev}**	**AIC$_c$**	**ΔAIC**	**W$_i$**
Damage					
Dead tree	+ Struct$_2$ + Compos$_1$ + Compos$_2$	0.30	148.68	0	0.98
Uprooted tree	+ Struct$_2$ + Compos$_1$	0.85	59.81	0	0.88
Broken trunk	+ Struct$_1$ + Compos$_1$	0.90	64.72	0	0.79
Bent trunk	+ Struct$_2$ – Compos$_2$	0.42	122.98	0	0.94
Inclined trunk	+ Struct$_1$ – Compos$_1$ + Compos$_2$	0.87	87.47	0	0.99
Tree without branches	+ Compos$_1$ + Compos$_2$	0.48	99.30	0	0.88
Secondary broken branches	+ Struct$_1$	0.49	37.39	0	0.54
Undamage tree	+ Compos$_2$	0.22	70.49	0	0.48
	– Struct$_2$ + Compos$_2$	0.35	40.64	5.54	0.23
Recovery					
Number of resprouts	– Compos$_1$ – Compos$_2$	0.89	62.19	0	0.96

n = 8. Response variables: numbers of individuals corresponding each category of damage and the number of resprouts and total basal area of resprouts as proxies of vegetation recovery capacity. Explanatory variables: scores of the first and second ordination axes reflecting plant assemblage's dissimilarities in species composition (Compos$_1$ and Compos$_2$) and vegetation structure (Struct$_1$ and Struct$_2$). On one hand, the first axis of the vegetation structure ordination (Struct$_1$) was positively related to leaf area index (LAI), average density of individuals (Intensity), total number of branches (No. branches), average height of emerging trees (Height), total number of individuals (No. individuals), and stand basal area (SBA); and negatively related to average nearest neighbor distance (Distance). On the other hand, the second axis of the vegetation structure ordination (Struct$_2$) was positively related to SBA and Height and negatively related to No. branches, No. individuals, Intensity, LAI and Distance. R^2_{dev}, fraction of the total deviance explained by a model when the Poisson error distribution was used and R^2 when the normal error distribution was used; AIC$_c$, sample-sized adjusted Akaike information criterion; ΔAIC, Akaike differences; and W$_i$, Akaike weights. Non-significant relationship was found for the total basal area of resprouts. Detailed information about these analyses are presented in the method section.

Table 3. Results of the linear model based on PIC relating species leaf traits and their resprouting capacity.

Parameters	**Coefficient**				**n**	**R^2**	**F; P - value**
Recovery	**CC**	**SLA**	**LFM**	**LD**			
Mean number of resprouts	**0.068**	-0.006	0.747	**3.007**	118	0.435	20.82; 0
Mean resprout basal area	0.107	-0.003	-1.975	-0.235	117	0.001	0.04; 0.99

R^2 is the R-squared measure of goodness of fit. The coefficients corresponding to a significant relationship ($P \leq 0.05$) are shown in bold. Detailed information about these analyses are presented in the methods section.

Table 4. Results of the linear model based on PIC relating species whole-plant traits and their type of damage and resprouting capacity.

Parameters	**Coefficient**			**n**	**R^2**	**F; P - value**
Damage	**Wood density**	**Height**	**Basal area**			
Uprooted tree	-2.192	-0.342	0.009	6	0.692	1.50; 0.42
Broken trunk	1.884	***0.333***	***-0.008***	8	0.793	5.09; 0.07
Bent trunk	-0.186	0.247	***-0.007***	12	0.317	1.24; 0.36
Inclined trunk	***-1.356***	**-0.549**	0.003	13	0.884	22.92; 0
Recovery						
Mean number of resprouts	-6.192	-0.121	0.007	79	0.025	0.62; 0.60
Mean resprout basal area	**-32.968**	**-7.955**	0.053	77	0.341	12.6; 0

R^2 is the R-squared measure of goodness of fit. The coefficients corresponding to a significant relationship ($P \leq 0.05$) are shown in bold, and marginal relationships ($0.05 < P \leq 1.00$) are shown in bold italic. Detailed information about these analyses are presented in the methods section. Insufficient PIC precluded the analyses corresponding to “dead tree”, “tree without branches”, “secondary broken branches” and “undamaged tree”.

Figures

Figure 1.

a), b) Sampling sites distribution along the pacific coast of Mexico with respect to the trajectory of Hurricane Patricia. The polygon represents the limits of the Chamela-Cuixmala Biosphere Reserve, and the squares and triangles represent the old growth forest and secondary forest plots, respectively.

Figure 2. Illustrations of the different categories of damage. Categories of damage (from a high to a low level of damage): 1) dead tree, 2) uprooted tree, 3) broken trunk, 4) bent trunk, 5) inclined trunk, 6) tree without branches, 7) secondary broken branches, and 8) undamaged tree.

Figure 3. non-Metric Multidimensional Scaling Ordinations mapping plant communities' dissimilarities in terms of species composition (A), vegetation structure (B), and vegetation damage (C).

The squares represent the centroids corresponding to each habitat type: old growth forest (OGF) and secondary forest (SEF). The vegetation attributes considered for the vegetation structure ordination were: leaf area index (LAI), average nearest neighbor distance (Distance), average density of individuals (Intensity), total number of branches (No. branches), average height of the emerging trees (Height), total number of individuals (No. individuals), and stand basal area (SBA). Between parenthesis is shown the Pearson correlation coefficient describing the relationship between vegetation attributes and ordination axes. The categories of damage considered for the vegetation damage ordination were (from high to low level of damage): dead tree, uprooted tree, broken trunk, bent trunk, inclined trunk, tree without branches, secondary broken branches, and undamaged tree.

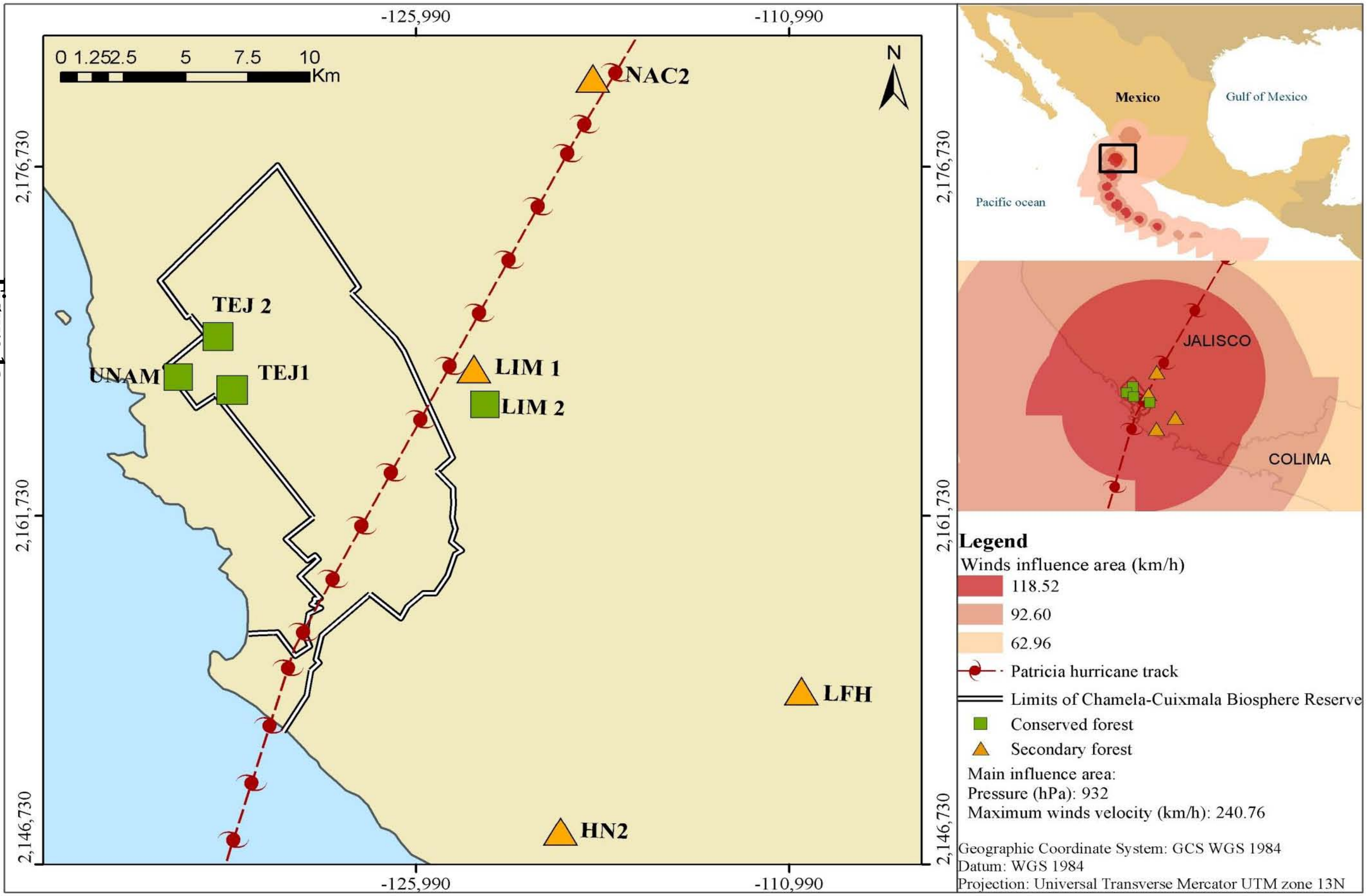
Figure 4. Aspect photos of the damage caused on vegetation for old growth forest (upper half of the box) and secondary forest (lower half of the box). Pictures b and c correspond to the rainy season whereas pictures a and d correspond to the dry season.

Figure 5. Distribution of individuals corresponding to old growth forest and secondary forest among the different categories of damage (above charts) and in relation to their height and basal area (below charts). The categories of damage considered were (from high

to low level of damage): 1) dead tree, 2) uprooted tree, 3) broken trunk, 4) bent trunk, 5) inclined trunk, 6) tree without branches, 7) secondary broken branches, and 8) undamaged tree.

Figure 6. Distribution of individuals corresponding to old growth forest and secondary forest with respect to their number of resprouts (above charts) and in relation to their height and basal area (below charts).

Figure 1a


-125,990
-110,990
2,176,730
2,161,730
2,146,730
0 1.25 2.5 5 7.5 10
Km
N
NAC2
TEJ 2
UNAM
TEJ1
LIM 1
LIM 2
LFH
HN2
Mexico
Gulf of Mexico
Pacific ocean
JALISCO
COLIMA
Legend
Winds influence area (km/h)
118.52
92.60
62.96
Patricia hurricane track
Limits of Chamela-Cuixmala Biosphere Reserve
Conserved forest
Secondary forest
Main influence area:
Pressure (hPa): 932
Maximum winds velocity (km/h): 240.76
Geographic Coordinate System: GCS WGS 1984
Datum: WGS 1984
Projection: Universal Transverse Mercator UTM zone 13N

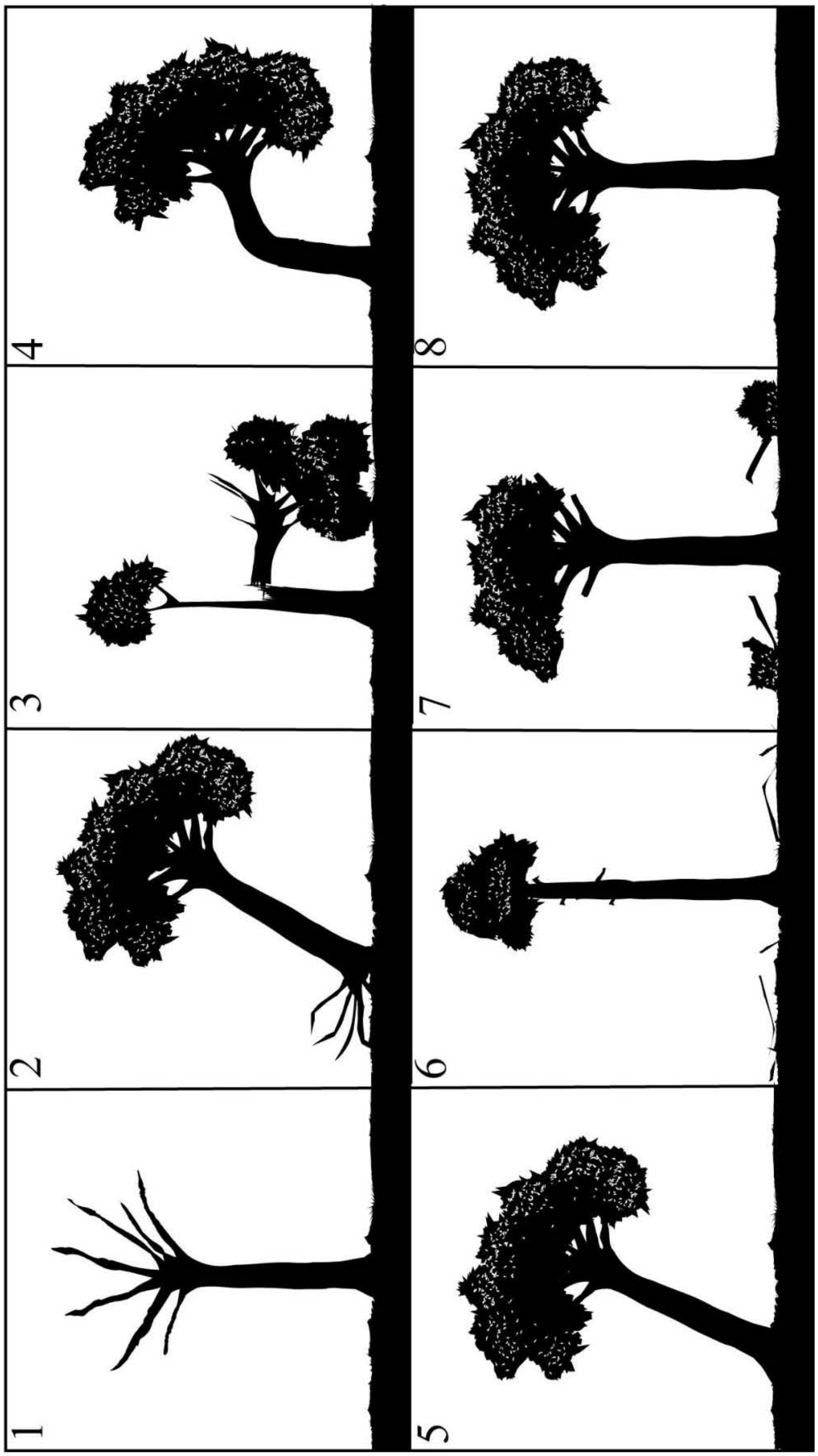


Figure 2

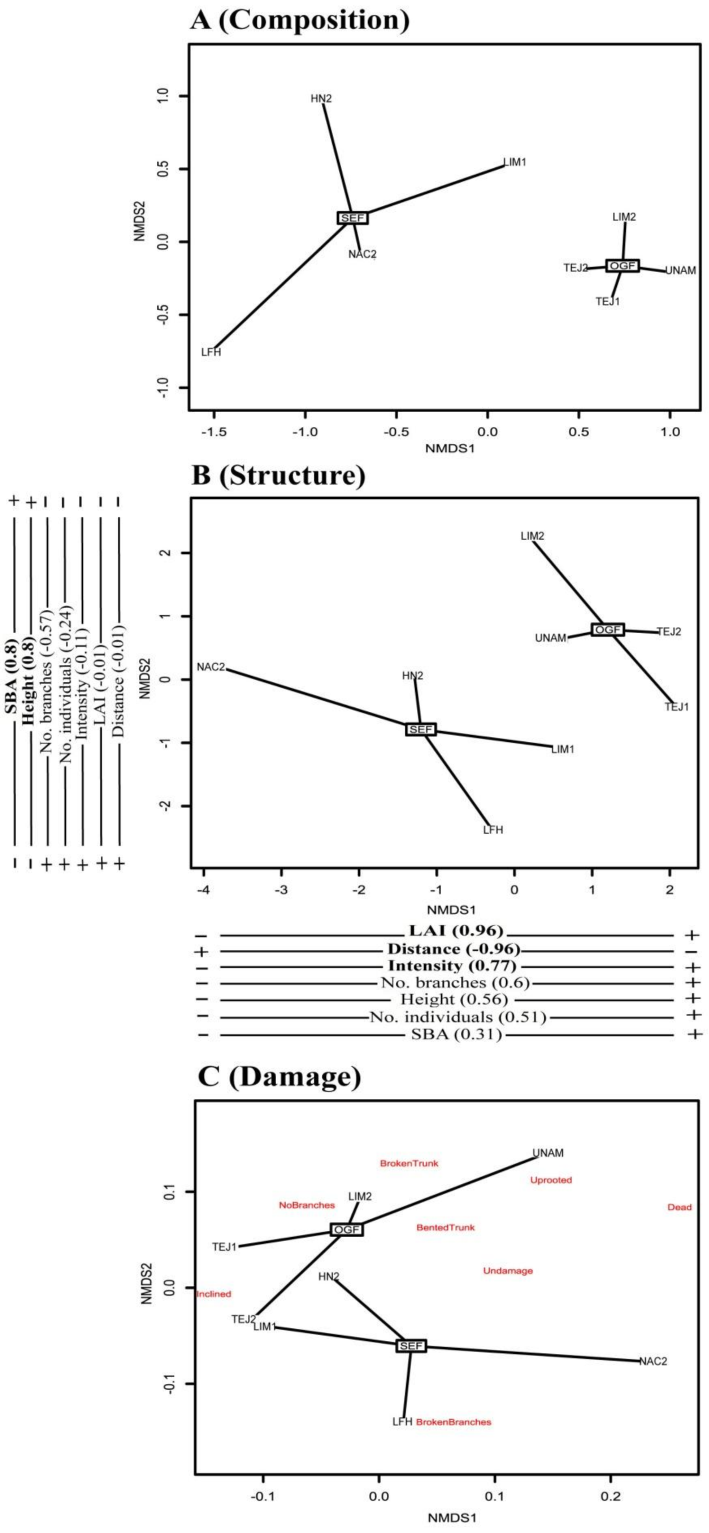

A (Composition)
HN2
LIM1
SEF
NAC2
LIM2
TEJ2
OGF
UNAM
TEJ1
LFH
NMDS2
NMDS1
1.0
0.5
0.0
-0.5
-1.0
-1.5
B (Structure)
SBA (0.8)
Height (0.8)
No. branches (-0.57)
No. individuals (-0.24)
Intensity (-0.11)
LAI (-0.01)
Distance (-0.01)
LIM2
OGF
TEJ2
UNAM
TEJ1
NAC2
HN2
SEF
LIM1
LFH
2
1
0
-1
-2
-3
-4
LAI (0.96)
Distance (-0.96)
Intensity (0.77)
No. branches (0.6)
Height (0.56)
No. individuals (0.51)
SBA (0.31)
C (Damage)
UNAM
BrokenTrunk
Uprooted
Dead
NoBranches
LIM2
OGF
BentedTrunk
TEJ1
Undamage
HN2
Inclined
TEJ2
LIM1
SEF
NAC2
LFH
BrokenBranches
0.1
0.0
-0.1
0.2

Figure 3

Figure 4

Figure 5

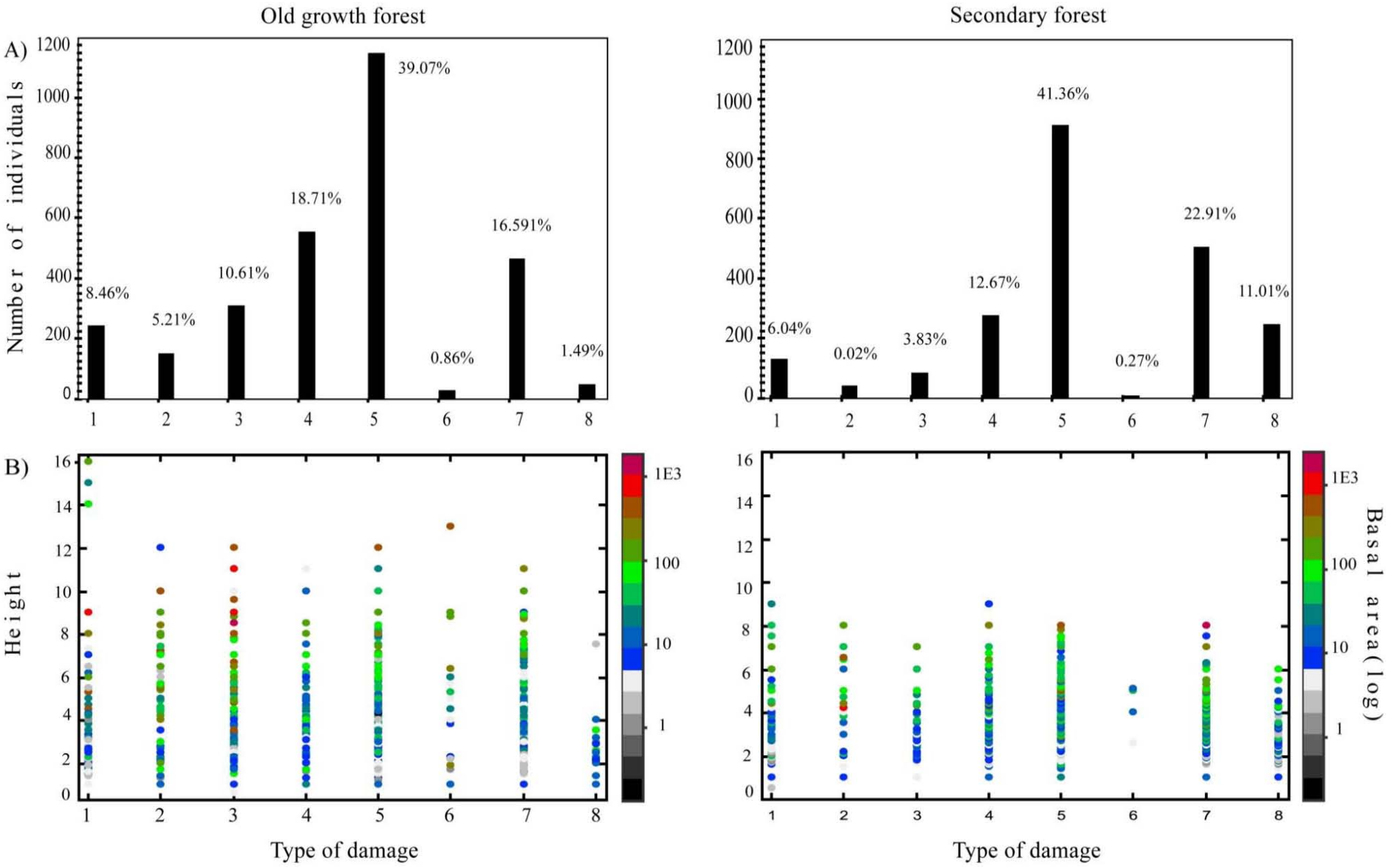
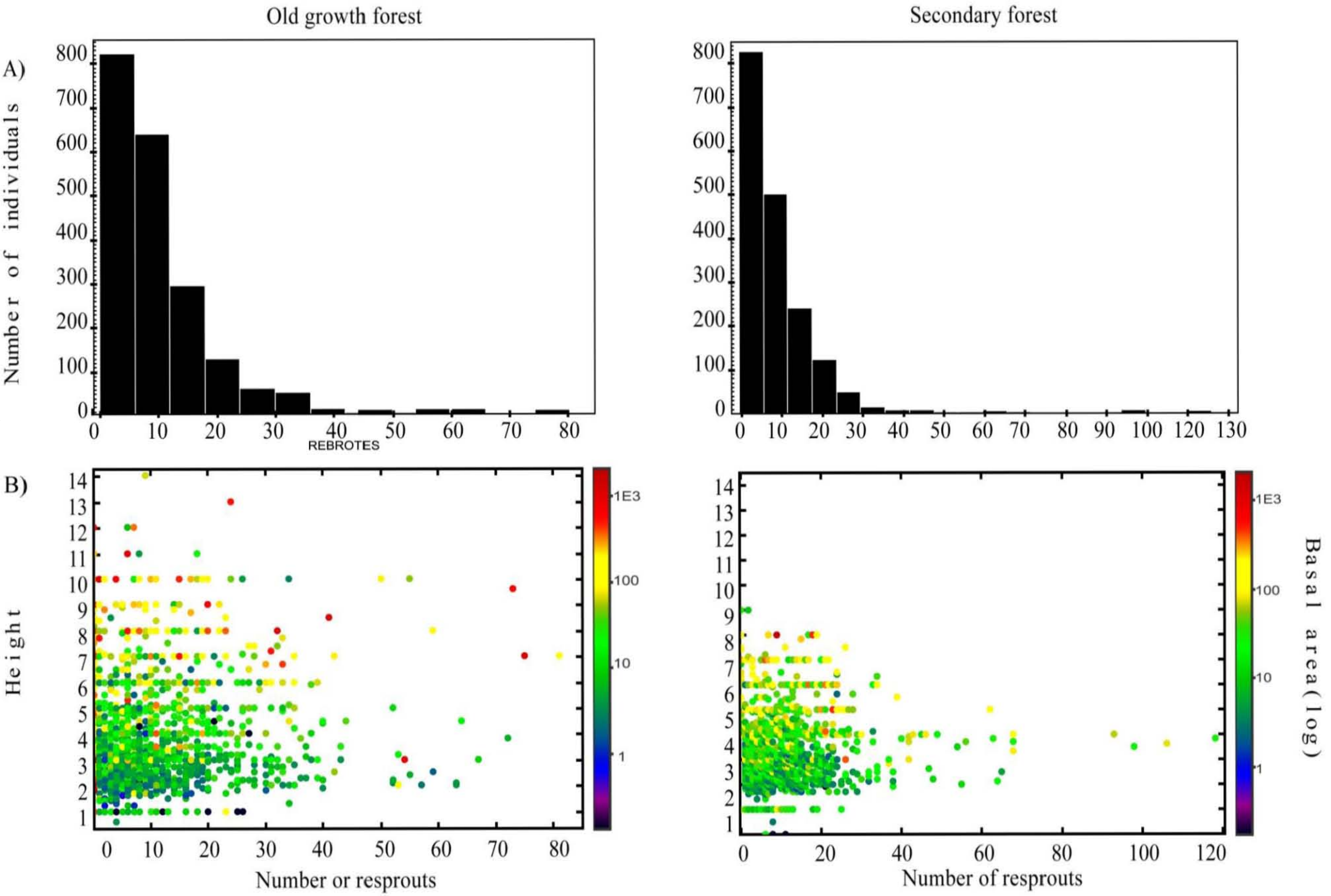

Old growth forest
Secondary forest
A)
Number of individuals
1200
1000
800
600
400
200
0
8.46%
5.21%
10.61%
18.71%
39.07%
0.86%
16.591%
1.49%
6.04%
0.02%
3.83%
12.67%
41.36%
0.27%
22.91%
11.01%
1
2
3
4
5
6
7
8
B)
Height
16
14
12
10
8
6
4
2
0
1E3
100
10
1
Basal area (log)
Type of damage
Type of damage

Figure 6


Old growth forest
Secondary forest
A)
Number of individuals
800
700
600
500
400
300
200
100
0
0
10
20
30
40
50
60
70
80
REBROTES
0
10
20
30
40
50
60
70
80
90
100
120
130
B)
Height
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
10
20
30
40
50
60
70
80
Number or resprouts
1E3
100
10
1
0
20
40
60
80
100
120
Number of resprouts
Basal area (log)

Supporting information legends

Figure S1. Chronogram containing all plant species considered in the analyses accounting for phylogenetic correlation. Branch lengths represent millions of years. The genera and species names are separated by an undercore. Scale bar = 50 myr.

Table S1. Abundance, preponderant type of damage and resprouting capacity for the most abundant species, on each type of habitat.

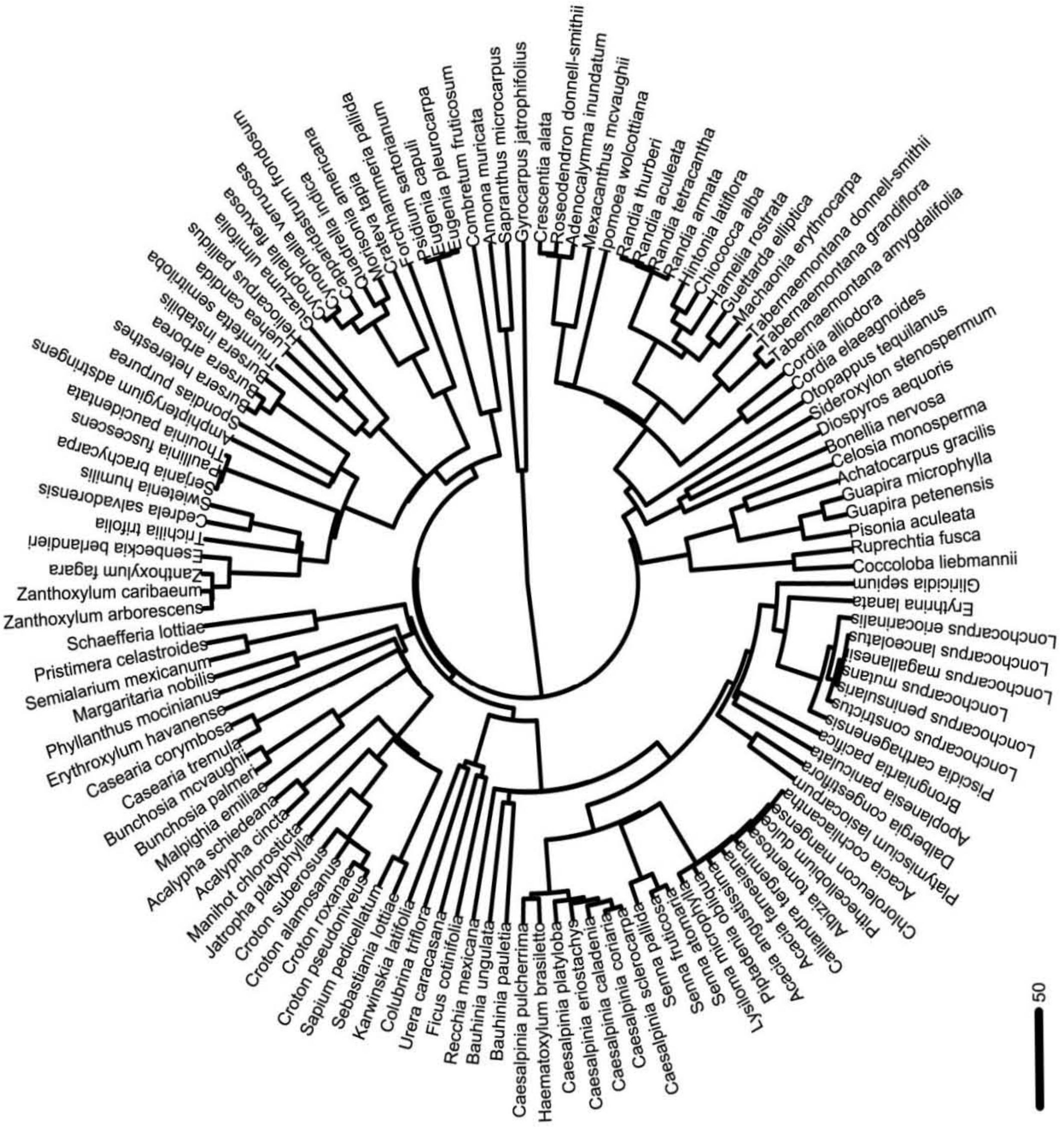

Zanthoxylum arborescens
Zanthoxylum caribaeum
Zanthoxylum fagara
Esenbeckia berlandieri
Trichilia trifolia
Cedrela salvadorensis
Swietenia humilis
Serjania brachycarpa
Paullinia fuscescens
Thouinia paucidentata
Amphipterygium adstringens
Spondias purpurea
Bursera heteresthes
Bursera arborea
Bursera instabilis
Triumfetta semitriloba
Luehea candida
Heliocarpus pallidus
Guazuma ulmifolia
Cynophalla flexuosa
Cynophalla verrucosa
Capparidastrum frondosum
Quadrella indica
Morisonia americana
Crateva tapia
Forchhammeria pallida
Psidium sartorianum
Eugenia capuli
Eugenia pleurocarpa
Combretum fruticosum
Annona muricata
Sapranthus microcarpus
Gyrocarpus jatrophifolius
Crescentia alata
Roseodendron donnell-smithii
Adenocalymma inundatum
Mexacanthus mcvaughii
Ipomoea wolcottiana
Randia thurberi
Randia aculeata
Randia tetracantha
Randia armata
Hintonia latiflora
Chiococca alba
Hamelia rostrata
Guettarda elliptica
Machaonia erythrocarpa
Tabernaemontana donnell-smithii
Tabernaemontana grandiflora
Tabernaemontana amygdalifolia
Cordia alliodora
Cordia elaeagnoides
Otopappus tequilanus
Sideroxylon stenospermum
Diospyros aequoris
Bonellia nervosa
Celosia monosperma
Achatocarpus gracilis
Guapira microphylla
Guapira petenensis
Pisonia aculeata
Ruprechtia fusca
Coccoloba liebmannii
Gliricidia sepium
Erythrina lanata
Lonchocarpus eriocarinalis
Lonchocarpus lanceolatus
Lonchocarpus magallanesii
Lonchocarpus mutans
Lonchocarpus peninsularis
Lonchocarpus constrictus
Piscidia carthagenensis
Brongniartia pacifica
Apoplanesia paniculata
Dalbergia congestiflora
Platymiscium lasiocarpum
Acacia cochliacantha
Chloroleucon mangense
Pithecellobium dulce
Albizia tomentosa
Calliandra tergemina
Acacia farnesiana
Acacia angustissima
Piptadenia obliqua
Lysiloma microphylla
Senna atomaria
Senna fruticosa
Senna pallida
Caesalpinia sclerocarpa
Caesalpinia coriaria
Caesalpinia caladenia
Caesalpinia eriostachys
Caesalpinia platyloba
Haematoxylum brasiletto
Caesalpinia pulcherrima
Bauhinia pauletia
Bauhinia ungulata
Recchia mexicana
Ficus cotinifolia
Urera caracasana
Colubrina triflora
Karwinskia latifolia
Sebastiania lottiae
Sapium pedicellatum
Croton pseudoniveus
Croton roxanae
Croton alamosanus
Croton suberosus
Jatropha platyphylla
Manihot chlorosticta
Acalypha cincta
Acalypha schiedeana
Malpighia emiliae
Bunchosia palmeri
Bunchosia mcvaughii
Casearia tremula
Casearia corymbosa
Erythroxylum havanense
Phyllanthus mocinianus
Margaritaria nobilis
Semialarium mexicanum
Pristimera celastroides
Schaefferia lottiae
50

Figure S1

Table S1. Abundance, preponderant type of damage and resprouting capacity for the most abundant species, on each type of habitat. Abundance (A), preponderant type of damage (D) and resprouting capacity (R) for the most abundant species, on each type of habitat (Secondary forest and Old growth forest).

Taxa	**Secondary forest**			**Old growth forest**		
	A	**D**	**R**	**A**	**D**	**R**
Acanthaceae						
Mexacanthus mcvaughii[a]	1	7	6/53.57	1	1	11/1.56
Achatocarpaceae						
Achatocarpus gracilis[a]	0	-	-	2	4	17/1.02
Amaranthaceae						
Celosia monosperma[a]	0	-	-	14	5	132/2.23
Anacardiaceae						
Amphipterygium adstringens[A]*	3	5	14/1.28	2	5	10/0.75
Spondias purpurea[A]*	0	-	-	4	5	49/0.90
Annonaceae						
Annona muricata[A]*	4	4	16/1.09	0	-	-
Sapranthus microcarpus[A]	6	5	44/1.05	0	-	-
Apocynaceae						
Tabernaemontana amygdalifolia[a]*	7	5	56/1.07	0	-	-
Tabernaemontana donnell-smithii[A]*	4	7	26/0.55	1	5	4/1.13
*Tabernaemontana grandiflora**	8	5	44/0.65	2	4	19/3.40
Bignoniaceae						
Adenocalymma inundatum[L]	1	8	10/1.46	0	-	-
Crescentia alata[A]*	10	7	40/64.46	0	-	-
Roseodendron donnell-smithii[A]*	5	5	37/0.69	0	-	-
Boraginaceae						
Cordia alliodora[A]*	12	5	58/1.21	2	3	17/2.28
C. elaeagnoides[A]*	1	5	9/2.21	11	1	74/2.54
Burseraceae						
Bursera arborea[A]*	0	-	-	2	3	7/1.42
B. heteresthes[A]*	0	-	-	3	4	15/0.7

						0
B. instabilis[A]*	3	4	9/0.23	5	5	41/2.72
Capparaceae						
Capparidastrum frondosum[a]*	1	7	0	0	-	-
Crateva tapia[A]*	1	4	5/0.85	0	-	-
Cynophalla flexuosa[a]	6	5	30/0.93	1	5	0
Cynophalla verrucosa	4	5	30/4.85	0	-	-
Forchhammeria pallida[A]*	2	7	25/1.13	3	7	7/0.31
Morisonia americana[A]*	1	5	4/2.96	0	-	-
Quadrella indica[a]	1	7	0	10	4	32/0.49
Celastraceae						
Pristimera celastroides[L]*	17	7	63/0.62	0	-	-
Schaefferia lottiae[a]	0	-	-	2	5	14/0.53
Semialarium mexicanum[L]	1	7	25/2.0	0	-	-
Combretaceae						
Combretum fruticosum[L]*	1	7	6/0.65	1	8	3/1.25
Compositae						
Otopappus tequilanus[L]	0	-	-	1	7	4/1.44
Convolvulaceae						
Ipomoea wolcottiana[A]*	1	3	8/0.47	2	2	5/4.68
Ebenaceae						
Diospyros aequoris[a]	0	-	-	2	5	5/0.56
Erythroxylaceae						
Erythroxylum havanense[A]*	2	2	8/0.22	1	5	11/1.72
Euphorbiaceae						
Acalypha cincta[a]	1	4	0	6	5	30/0.80
Acalypha schiedeana[a]	1	4	9/1.29	1	1	10/0.47
Croton alamosanus[a]*	24	4	131/42.32	3	4	19/1.36
C. pseudoniveus[A]	4	5	23/31.79	4	5	28/1.45
C. roxanae[A]	8	5	112/1.26	78	5	559/0.97
C. suberosus[a]	11	5	58/0.95	97	5	660/2.48
Jatropha platyphylla[a]*	3	5	7/5.87	0	-	-
Manihot chlorosticta[L]	0	-	-	2	8	3/0.29

Margaritaria nobilis^{A}*	1	7	5/0.63	0	-	-
Phyllanthus mocinianus	0	-	-	3	4	27/1.15
Sapium pedicellatum^{A}*	2	3	18/0.58	1	5	23/2.02
Sebastiania lottiae^{A}	0	-	-	14	4	38/3.37
Hernandiaceae						
Gyrocarpus jatrophifolius^{A}*	4	3	9/8.99	1	3	4/3.78
Leguminosae						
Acacia angustissima^{A}	1	5	0	0	-	-
A. cochliacantha^{a}*	29	5	205/13.78	0	-	-
A. farnesiana^{A}	2	5	6/23.32	0	-	-
Albizia tomentosa^{A}	3	5	4/1.24	0	-	-
Apoplanesia paniculata^{A}*	1	5	6/0.19	59	5	585/1.92
Bauhinia pauletia^{a}*	0	-	-	1	5	0.00
B. ungulata^{A}*	23	5	95/1.56	0	-	-
Brongniartia pacifica^{a}	3	7	12/6.40	1	7	72/5.20
Caesalpinia caladenia^{a}*	0	-	-	2	5	11/2.07
C. coriaria^{A}*	33	7	161/67.50	3	5	36/1.73
C. eriostachys^{A}*	0	-	-	14	3	191/2.68
C. platyloba^{A}*	0	-	-	5	5	47/4.59
*C. pulcherrima**	8	5	22/0.71	20	5	99/0.78
C. sclerocarpa^{A}*	2	1	16/4.75	7	3	45/1.65
Calliandra tergemina^{a}	0	-	-	2	5	33/1.24
Chloroleucon mangense^{A}*	0	-	-	2	2	3/4.53
Dalbergia congestiflora^{A}*	0	-	-	1	5	1/0.03
Erythrina lanata^{A}*	0	-	-	1	2	6/1.65
Gliricidia sepium^{A}*	3	5	26/0.84	0	-	-
Haematoxylum brasiletto^{A}*	108	5	643/79.93	25	5	144/1.69
Lonchocarpus constrictus^{A}*	19	5	98/1.01	3	7	18/3.43
L. eriocarinalis^{A}*	22	5	129/0.80	7	5	38/0.6

						3
L. lanceolatus^{A}	1	7	10/0.71	23	5	271/1.32
L. magallanesii^{A}*	6	5	33/0.87	0	-	-
L. mutans^{A}*	5	4	34/0.87	2	5	35/4.88
L. peninsularis^{A}*	11	4	30/0.40	0	-	-
Lysiloma microphylla^{A}*	3	5	27/0.44	6	5	71/1.53
Piptadenia obliqua^{A}*	1	5	24/1.63	15	5	115/2.05
Piscidia carthagenensis^{A}*	8	5	32/2.31	3	2	26/3.66
Pithecellobium dulce^{A}*	2	5	14/91.76	0	-	-
Platymiscium lasiocarpum^{A}*	7	5	52/1.01	0	-	-
Senna atomaria^{A}*	9	7	48/1.08	0	-	-
S. fruticosa^{a}	1	3	7/0.88	0	-	-
S. pallida^{a}	32	5	93/34.20	5	5	48/0.73
Malpighiaceae						
Bunchosia mcvaughii^{a}	1	4	13/1.11	0	-	-
B. palmeri^{a}*	1	5	2/1.90	2	3	15/9.41
Malpighia emiliae	0	-	-	3	5	25/0.73
Malvaceae						
Guazuma ulmifolia^{a}*	14	7	47/1.68	1	5	30/0.64
Heliocarpus pallidus^{A}*	5	5	65/1.62	15	5	78/5.49
Luehea candida^{A}*	1	5	17/2.43	0	-	-
Triumfetta semitriloba^{a}	1	2	3/0.11	0	-	-
Meliaceae						
Cedrela salvadorensis^{A}*	9	5	89/1.72	0	-	-
Swietenia humilis^{A}	1	7	9/2.54	0	-	-
Trichilia trifolia^{A}*	7	7	28/0.37	4	5	14/21.06
Moraceae						
Ficus cotinifolia^{A}	0	-	-	1		55/0.67
Myrtaceae						
Eugenia capuli^{a}*	64	5	353/0.62	0	-	-
E. pleurocarpa^{a}	2	5	36/2.28	0	-	-
Psidium sartorianum^{A}*	41	5	341/0.46	2	5	5.00

Nyctaginaceae						
Guapira microphylla	1	4	5/0.29	10	4	37/2.06
G. petenensis^{A}	3	5	13/0.75	12	5	87/1.63
Pisonia aculeata^{L}*	18	7	139/2.48	1	4	6/3.82
Polygonaceae						
Coccoloba liebmannii^{A}*	7	7	24/3.10	3	5	5/2.79
Ruprechtia fusca^{A}*	1	3	0	7	5	43/1.40
Primulaceae						
*Bonellia nervosa**	8	7	33/8.11	15	7	8/0.09
Colubrina triflora^{A}*	3	5	19/0.93	3	3	19/1.31
Karwinskia latifolia^{a}	1	5	2/0.31	1	5	5/0.46
Rubiaceae						
Chiococca alba^{a}	1	5	12/1.48	0	-	-
Guettarda elliptica^{A}*	2	4	10/0.73	5	5	42/1.22
Hamelia rostrata^{a}	0	-	-	3	4	42/1.54
Hintonia latifolia^{A}*	0	-	-	6	5	41/1.11
Machaonia erythrocarpa^{a}	1	4	11/0.72	2	5	17/1.45
Randia aculeata^{a}*	1	5	7/0.49	2	5	7/0.52
R. armata^{L}*	3	5	36/1.67	0	-	-
R. tetracantha^{L}*	5	4	40/1.31	8	4	17/0.54
R. thurberi^{A}*	0	-	-	3	5	7/1.88
Rutaceae						
Esenbeckia berlandieri^{A}*	4	5	33/0.94	0	-	-
Zanthoxylum arborescens^{A}*	0	-	-	3	7	2/0.13
Z. caribaeum^{A}*	3	5	6/5.74	0	-	-
Z. fagara^{A}*	33	5	309/1.78	0	-	-
Salicaceae						
Casearia corymbosa^{a}*	20	5	196/1.17	2	5	3/0.11
C. tremula^{A}*	1	8	5/0.42	2	5	6/0.43
Sapindaceae						
Paullinia fuscescens^{L}	1	8	0	0	-	-
Serjania brachycarpa^{L}	1	8	0	21	7	83/0.62
Thouinia paucidentata^{A}*	5	5	70/1.06	27	5	428/5.41

Sapotaceae						
Sideroxylon stenospermum^{A}	1	5	1/0.07	1	7	5/0.31
Simaroubaceae						
Recchia mexicana^{A}*	0	-	-	2	4	42/3.14
Urticaceae						
Urera caracasana^{A}*	0	-	-	6	5	3/0.08

Abundance (A), mean number of individuals; Damage (D), most common category of damage (mode); and Recovery (R), mean number of resprouts / mean resprout basal area. Categories of damage (from a high to a low level of damage): 1) dead tree, 2) uprooted tree, 3) broken trunk, 4) bented trunk, 5) inclined trunk, 6) tree without branches, 7) secondary broken branches, and 8) undamaged tree. All the listed species were included in the analysis considering leaf traits and the ones marked with * were included in the analysis considering whole-plant traits. A = tree, a = shrub and L= lianas.

The taxonomic designation of species follows “The Plant List” (http://www.theplantlist.org).

CAPÍTULO III

Consideraciones finales

La historia de uso de suelo interacciona con las fuerzas naturales para influenciar la severidad de las perturbaciones y la tasa de recuperación en los bosques tropicales. Esta recuperación será más lenta cuando aparte del efecto del huracán sobre el dosel, el suelo ha sido previamente alterado por las actividades humanas como pastoreo o remoción del suelo (Chazdon 2003). Tal sería el caso de los bosques secundarios del BTS, en donde los procesos de lluvia y dispersión de semillas que resultan claves en la regeneración, podrían verse también disminuidos a causa de la disminución en la abundancia de especies animales (Janzen 1990).

Ante un aumento en la frecuencia/intensidad de huracanes en el BTS, los efectos de este aumento se pueden combinar con las perturbaciones humanas previas produciendo un nuevo y sorpresivo estado del sistema (Paine et al. 1998). Esto sucede cuando una segunda perturbación ocurre en un momento en que el sistema aún no se ha recuperado de la primera perturbación, conduciendo a dicho sistema a un nuevo estado de larga duración. En nuestro estudio, el huracán Patricia (categoría 5) llega cuatro años después del huracán Jova (categoría 3), pero no sabemos hasta qué punto el sistema se había recuperado o no del paso de Jova. Esta combinación de perturbaciones, acordes al actual contexto de cambio climático, no tiene precedentes en la historia reciente de este BTS y sus consecuencias pueden ser impredecibles, aparecer lentamente y ser difíciles de detectar en nuestra escala temporal (Dale et al. 2001).

Los daños a los ecosistemas de Bosque Tropical Seco van en aumento, y son igual de graves tanto para los bosques conservados como para los que ya han sido alterados. De acuerdo a lo observado en este estudio, los huracanes de alta intensidad, pueden incluso causar más daños en los bosques conservados que en los bosques secundarios. Conocer el acuerdo a lo observado en este estudio, los huracanes de alta intensidad pueden incluso causar más daños en los bosques conservados que en los bosques secundarios. Conocer el nivel de cambio que estas nuevas presiones provocan en los ecosistemas así como predecir cómo sería este cambio en el largo plazo, resulta fundamental para crear estrategias de manejo y mitigación enfocadas tanto en las actividades antropogénicas como en el cambio climático, ya que, aunque los fenómenos climáticos no pueden evitarse, sí se pueden mitigar los disturbios derivados de estos.

Así, los planes de manejo deben contemplar estrategias que ayuden a mitigar los impactos ya causados, coadyuvando, entre otras cosas, a la recuperación de la vegetación. En los planes de manejo de las reservas de Bosque Seco, o en los objetivos de reforestación de la Comisión Nacional Forestal, no está contemplado el enfoque de la evaluación y recuperación de las funciones en los ecosistemas, por lo que en muchas ocasiones se enfocan los esfuerzos en ciertos aspectos como la recuperación o mantenimiento del suelo o del ciclo de agua, aunque esto no siempre garantiza que la vegetación esté cumpliendo sus funciones ecosistémicas originales.

En este sentido, dado que los atributos funcionales de la vegetación van de la mano con los servicios ecosistémicos, su evaluación sería útil para saber cómo está funcionando la vegetación en los bosques. La evaluación de atributos funcionales cuya medición sea práctica, así como la estandarización de los valores que ayuden a evaluar la salud y buen funcionamiento de los ecosistemas, son herramientas que facilitarían enormemente la correcta acción de los órganos del gobierno e instituciones responsables del manejo y conservación de los mismos.

Aunado a la serie de acciones propuestas anteriormente, también se propone generar estrategias de manejo que ayuden al bosque y a la población que habita a los alrededores a evitar futuros riesgos y disturbios. Ante el paso de un huracán, por ejemplo, la gran cantidad de materia orgánica que queda acumulada en el suelo, sumada a las condiciones ambientales de la época de secas, hacen que los bosques queden más susceptibles a los incendios forestales. Realizar limpiezas de restos de ramas y árboles muertos que quedan en el bosque o en lugares estratégicos, podría entonces ayudar a evitar que los incendios ocurran o que sean muy grandes.

Es posible que este tipo de disturbios ocurra con mayor frecuencia en el futuro, y el cambio en los ecosistemas será inevitable, sin embargo, el mantenimiento de los bosques conservados puede garantizar que los cambios a largo plazo sean menos drásticos. En el caso de la costa de Jalisco, los continuos de bosque que aún permanecen podrían amortiguar dichos cambios así como facilitar la regeneración del sistema. Además, estos bosques junto con la geomorfología propia de la zona, podrían también amortiguar la fuerza de los vientos y el agua, disminuyendo la intensidad de los huracanes en su paso al interior del país. Esto destaca la enorme importancia de generar planes de manejo, mitigación y conservación adecuados para preservar las áreas naturales conservadas de los paisajes tropicales antropogénicos.

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