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Relaciones entre tendencias climáticas, patrones fenológicos, y la abundancia del quetzal en El Triunfo, Chiapas

Tesis
Presenta como requisito parcial para optar al grado de Doctor en Ciencias en Ecología y Desarrollo Sustentable
Con orientación en Conservación de la Biodiversidad

Por

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2022

El Colegio de la Frontera Sur

San Cristóbal de Las Casas, Chiapas, a 27 de enero de 2022.

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para obtener el grado de **Doctor en Ciencias en Ecología y Desarrollo Sustentable**

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AGRADECIMIENTOS

Gracias a mi directora Dra. Paula Enríquez y a los miembros del comité: Dra. Guadalupe Williams-Linera, Dr. Darío Navarrete, Dr. Esteban Pineda y Dr. Miguel Martínez-Morales (†), por todo su apoyo. Los sinodales del examen de grado: Dr. Eduardo Naranjo Piñera, Dr. José Luis Rangel Salazar y Dra. Griselda Escalona Segura, por sus comentarios para mejorar la tesis. Marco Domínguez y Nathalia Castillo por su ayuda con el trabajo de campo, Raúl Vázquez por su ayuda con el análisis estadístico, Rubén Martínez con la identificación de especies de árboles, y mi papá, A.C. Wootton y Fabiola por revisar la gramática de los artículos, capítulos y documentos. También agradezco a los involucrados con el monitoreo de especies prioritarias en El Triunfo: los guardaparques y administradores de la reserva, estudiantes como parte de su servicio social, investigadores y trabajadores de Asociaciones Civiles Ambientales en Chiapas. A los directores, administradoras, cocineras y guardaparques de la reserva por su ayuda con el trabajo de campo y la logística: Juan Carlos Castro, Alexer Vázquez, Janette González, Rossana Megchun, Edilberto López, Abinaham López, Gilberto Argueta, Ramiro Gálvez, Ismael Gálvez, Adolfo Carbajal, Anelfo Gálvez, Joel Gómez, Roberto Gálvez, Rubí Gálvez, Luz Gálvez y Leticia Serrano. Raymundo por el ánimo a lo largo del proyecto y a mis compañeras de casa Fabiola y Sonia por sus incansables distracciones, y también por ayudar con el análisis de datos de lluvia y otras tantas cosas. El trabajo de campo y la recolección de frutos contaron con el permiso de la CONANP y SEMARNAT (No. SGPA/DGVS/8055/19). El proyecto recibió fondos fiscales del Departamento de Conservación de la Biodiversidad de El Colegio de la Frontera Sur y yo recibí una beca de doctorado del CONACyT (No. 884660) y de CONACyT-OEA-AMEXCID 2018.

INDÍCE

RESUMEN GENERAL

El cambio climático está influyendo en los procesos ecológicos en los ecosistemas de montañas tropicales tales como la fenología reproductiva de los árboles. Se hipotetizó que estos cambios también están ocurriendo en el bosque nuboso de la Reserva de la Biosfera El Triunfo, Chiapas. Los objetivos de esta tesis fueron determinar (1) las características de las tendencias climáticas de ~30 años en la Sierra Madre, (2) las relaciones entre el clima y los patrones de producción de flores y frutos, y (3) las relaciones entre la abundancia de frutos, la composición de especies de árboles que producen recursos alimentarios para el quetzal y la abundancia espacial y temporal de quetzales, en el polígono 1 de El Triunfo. Los métodos incluyeron análisis de tendencias de temperatura y lluvia, percepción remota de la cobertura vegetal, modelado espacial de la evapotranspiración actual, y observaciones de campo. Se realizaron mediciones de campo de especies de árboles y observaciones fenológicas durante 17 meses entre 2019-2021. También se incluyeron los datos mensuales de abundancia del quetzal recolectados desde 2010 hasta 2021, y se realizaron comparaciones con la abundancia del quetzal y frutos de 1991-1993. Los datos de campo se analizaron mediante correlaciones y estadísticas circulares. Desde 1990, las temperaturas mínimas diarias aumentaron, mientras que las temperaturas máximas disminuyeron y las tendencias significativas de la temperatura media en general fueron más frías en la Sierra Madre. El comienzo de las estaciones húmeda y seca se desplazó más temprano en el año y las lluvias en la estación húmeda aumentaron. Estas tendencias climáticas ocurrieron durante un periodo de aumentos en la extensión y densidad de la vegetación regional y la evapotranspiración, cambios en las condiciones oceánicas (aumentos en las temperaturas de la superficie del mar, y un cambio de la fase positiva a negativa de la Oscilación Decadal del Pacífico) y atmosféricas (aumentos en el CO_2). Las tendencias climáticas descritas en la Sierra Madre parecen estar afectando los patrones fenológicos de las especies arbóreas. La fecha promedio de la producción máxima estacional de frutos en 2019-20 ocurrió antes (12 de marzo) que en 1992 (29 de marzo) y 1993 (4 de mayo). También hubo una reducción en la cantidad de frutos después del huracán Eta en noviembre de 2020. Los cambios en los patrones de presencia de frutos podrían deberse a lluvia y nubosidad mayores o su ocurrencia más temprana en el año, y posiblemente estarían relacionados con un mayor consumo de frutos maduros por parte de los frugívoros en El Triunfo. Entre 2019 y 2021, la abundancia general del quetzal en el bosque nuboso estuvo correlacionada con el número de frutos maduros, la biomasa de los frutos, el número de especies de árboles con frutos, el número de frutos de la familia Lauraceae (marginalmente), y entre 2013-2020 con la lluvia mensual. La abundancia local del quetzal (en 3 ha) se correlacionó espacialmente con la biomasa de frutos de Lauraceae, la diversidad de especies de árboles, la distancia a las cañadas y marginalmente con el número de árboles de Lauraceae por hectárea. Estas características asociadas a la abundancia del quetzal en los bosques nubosos fueron generalmente mayores en las áreas riparias y los fondos de los valles, y menores en los bosques secundarios, laderas y crestas de los valles. Sin embargo, la abundancia de quetzales no difirió significativamente entre estas áreas, lo que sugiere que la diversidad local de especies de árboles, patrones de producción de frutos y características físicas influyen en el movimiento y abundancia de quetzales. Los datos y resultados de este proyecto se pueden utilizar para mostrar la importancia de mantener la alta diversidad de especies arbóreas y la riqueza de especies de la familia Lauraceae para la supervivencia de las poblaciones de quetzal en El Triunfo, explicar la abundancia de otros frugívoros en El Triunfo, proporcionar información para la restauración de los hábitats del bosque nuboso, y se pueden comparar con los cambios ecológicos regionales en otras Reservas de la Biosfera en la Sierra Madre y la costa de Chiapas.

Palabras Claves: bosque nuboso, clima, frutos, hábitat reproductivo, relaciones ecológicas

CAPÍTULO 1

Frutos de *Nectandra rudis*. Foto de Allen Wootton.

INTRODUCCIÓN GENERAL

Las influencias en el clima de Chiapas como la atmosférica (Liverman y O'Brien 1991), la oceánica (Méndez-González et al. 2010) y la cobertura del suelo (Lawton et al. 2001) han ido cambiando desde 1990 (NOAA 2020a, Lluch-Cota et al. 2013, Bonilla-Moheno y Aide 2020), por lo que podrían haber ocurrido tendencias (aumento/decremento o en el tiempo de la temporada húmeda) en la temperatura y en la lluvia en la Sierra Madre de Chiapas. Estas tendencias podrían estar afectando procesos ecológicos en los bosques nubosos de la Reserva de la Biosfera El Triunfo (González-García et al. 2017), ubicada en esta cordillera costera del Pacífico. Sin embargo, en México pocos estudios se han centrado en cambios ecológicos a largo plazo (~30 años) con relación a las tendencias climáticas en estos bosques tropicales de mayor altitud.

Los factores que influyen en la producción de flores y frutos en los bosques tropicales húmedos aún se comprenden menos que en los bosques tropicales estacionalmente secos o en los bosques templados (Mendoza et al. 2017, Pau et al. 2020). Una combinación compleja de condiciones bióticas y abióticas puede afectar a comunidades enteras de especies de árboles o especies individuales dentro de la comunidad (Pau et al. 2011). Sin embargo, los estudios fenológicos en bosques tropicales húmedos se han incrementado recientemente, mostrando relaciones entre los aspectos del clima y la fenología. Por ejemplo, se han registrado correlaciones entre la producción anual de flores y frutos, y los patrones de lluvia, humedad, temperatura y radiación solar en un bosque tropical húmedo de montaña en Colombia (Corredor-Londoño et al. 2020); y los cambios en la producción de frutos se han relacionado con las tendencias en la lluvia en un bosque de montaña en África (Dunham et al. 2018).

Los quetzales (*Pharomachrus mocinno* Trogonidae) a menudo migran altitudinalmente o a lo largo de las elevaciones del bosque nuboso de montaña para seguir la producción de frutos (Solórzano et al. 2000, Bustamante et al. 2010). Los cambios en los patrones de producción de frutos, influenciados por las tendencias climáticas en la Sierra Madre, pueden estar afectando los patrones de abundancia mensual del quetzal en su hábitat reproductivo en los bosques nubosos de El Triunfo. Entonces el periodo y el éxito reproductivo del quetzal, así como las interacciones ecológicas dentro del bosque nuboso pueden verse afectadas (Carleton y Smith 2016).

Esta tesis explora comparaciones y relaciones de ~30 años entre los cambios de temperatura y lluvia en la Sierra Madre (Capítulo 2), producción de flores y frutos en especies de árboles del bosque nuboso (Capítulo 3), y la abundancia espacial y temporal de quetzales en su hábitat reproductivo en El Triunfo (Capítulo 4). El capítulo final (5) proporciona una conclusión de los resultados y recomendaciones para la conservación tanto de los recursos alimentarios del quetzal como de esta especie en la Sierra Madre.

Parte 1. Cambio climático en la Sierra Madre de Chiapas

Cambios en el clima de Mesoamérica

Durante los últimos 100 años se han producido cambios en las temperaturas y las lluvias en Mesoamérica (Aguilar et al. 2005, Murray-Tortarolo 2020). Sin embargo, las tendencias han variado según el periodo de tiempo y región (Fuentes-Franco et al. 2015, Murray-Tortarolo et al. 2017), lo que refleja una mezcla compleja y cíclica de procesos climáticos que influyen en diferentes regiones de Mesoamérica (Fuentes-Franco et al. 2015). Desde 1970, las temperaturas en general han aumentado en México (Murray-Tortarolo 2020) y en América Central (Aguilar et al. 2005), debido al incremento de las temperaturas máximas y menores aumentos en las temperaturas mínimas (Englehart y Douglas 2005, Mateos et al. 2016).

Las tendencias de las lluvias en general han sido positivas en Mesoamérica, especialmente durante la temporada húmeda, y los eventos de lluvia se han intensificado (Aguilar et al. 2005). Sin embargo, algunas áreas han registrado tendencias negativas (Aguilar et al. 2005, Mateos et al. 2016), y las regiones montañosas presentan situaciones aún más complejas (Pounds et al. 1999, Barradas et al. 2010). En los bosques montañosos de Veracruz, se registraron tendencias significativas en las lluvias durante la estación seca entre 1950-2000, pero las tendencias fueron positivas (incrementos) o negativas (disminuciones) según la ubicación (Barradas et al. 2010). En general, las lluvias se incrementaron desde el final de la estación seca y durante la mayor parte de la estación húmeda, y hubo una tendencia más seca durante los meses al comienzo de la estación seca (Barradas et al. 2010). Las cantidades de niebla también aumentaron en altas elevaciones y disminuyeron en bajas elevaciones, posiblemente debido a cambios en la cobertura del suelo (Barradas et al. 2010). En la región del Pacífico de Chiapas, las precipitaciones disminuyeron en la región costera de baja elevación del Soconusco entre 1960-2012 y aumentaron en las áreas más cercanas a la Sierra Madre (Escalante-Sandoval y Amores-Rovelo 2014).

Influencias a gran escala en el clima de la Sierra Madre de Chiapas

El clima de Chiapas está influenciado en gran medida por procesos a escala global, pero también por las características regionales de la vegetación (Hewitson y Crane 1992). Las mayores cantidades de lluvia ocurren de junio hasta octubre, y esta lluvia depende del movimiento de la Zona de Convergencia Intertropical hacia el norte, que trae humedad del Caribe y del Golfo de México (Brito-Castillo 2012). Las temperaturas de la superficie del mar han ido aumentando desde 1975 en las áreas más cercanas a la costa este de México (Lluch-Cota et al. 2013); ésto podría aumentar el vapor del agua atmosférico a través de una mayor evaporación (Aguilar et al. 2005). La Oscilación Decadal del Pacífico es otra influencia oceánica en el clima de Chiapas y ha cambiado de una fase positiva a principios de la década de 1990 a una fase negativa de la década del 2000 (NOAA 2020b). Méndez-González et al. (2010) determinaron que, durante el último siglo en México, la fase negativa de la Oscilación Decadal del Pacífico se ha asociado con temperaturas máximas diarias bajas, aumentos en las temperaturas mínimas diarias y mayores cantidades de lluvia en el sur de México.

Los aumentos de CO_2 atmosférico también pueden haber contribuido a las tendencias climáticas en la Sierra Madre. Liverman y O'Brien (1991) predijeron que la duplicación de los niveles de CO_2 de cantidades registradas en 1990 causaría aumentos en las temperaturas durante todo el año, aumentos en las precipitaciones durante la estación húmeda y disminuciones al inicio de la estación seca en algunas regiones de Chiapas. En 30 años, de 1990 a 2020, los niveles de CO_2 atmosférico han aumentado de 350 ppm a 415 ppm (NOAA 2020a).

Influencias de la cobertura del suelo regional en el clima de la Sierra Madre

Además de las influencias a gran escala, los cambios regionales en la vegetación pueden estar influyendo en las tendencias de las temperaturas y las lluvias en la Sierra Madre. El suelo sin cubierta vegetal generalmente tiene un flujo de calor sensible más alto y las áreas de vegetación densa presentan un flujo de calor latente más alto (Ray et al. 2006). La tala a gran escala de bosques y otra vegetación puede ocasionar que la nubosidad orográfica aumente en elevación debido a este cambio en el balance energético de flujo de calor latente a sensible (Lawton et al. 2001). La vegetación densa también generalmente tiene cantidades más altas de evapotranspiración, debido a que las raíces más profundas llegan al agua subterránea, menor escorrentía de agua superficial, mayor captura de lluvia y mayor cobertura de hojas (Kleidon et al. 2000). La evapotranspiración puede aportar una gran cantidad de vapor de agua a la atmósfera desde los bosques y afectar las cantidades de precipitación (Durán-Quesada et al. 2012, Sheil 2018).

Las tendencias en la vegetación han ido cambiando en la Sierra Madre y en las regiones adyacentes de menor elevación (Depresión Central y costa del Pacífico). Entre 1970-1990, esta región experimentó una gran cantidad de deforestación (Richter 2000), con tasas anuales de 3.35 % en la Sierra Madre entre 1970-2000 (Solórzano et al. 2003). A principios de la década del 2000, se esperaba que esta tendencia continuara (Solórzano et al. 2003); sin embargo, entre los periodos 1990-2000 y 2000-2006, las tasas anuales de deforestación disminuyeron en la Depresión Central (0.15 a 0.06 % respectivamente; Vaca et al. 2012) y en los bosques de las montañas de Chiapas (0.22 a 0.07 % respectivamente; Vaca et al. 2012). Entre 2001-2014, hubo tendencias crecientes en la cobertura forestal en la mayoría de las áreas cercanas a la Sierra Madre, con una tendencia positiva similar en otras partes de México (Bonilla-Moheno y Aide 2020).

Estos cambios medidos o potenciales en las influencias climáticas regionales y de gran escala indican un clima dinámico y cambiante en la Sierra Madre desde el establecimiento de la Reserva de la Biosfera El Triunfo en 1990. Los cambios en la temperatura y las lluvias pueden estar influyendo en los procesos ecológicos en los bosques nubosos de la región, incluyendo los patrones fenológicos de las especies arbóreas (Chapman et al. 2005, Barnes 2015, Dunham et al. 2018).

Parte 2. Patrones fenológicos en el bosque nuboso de El Triunfo

Patrones fenológicos en los bosques nubosos tropicales

En las regiones tropicales de América, se han observado varios patrones fenológicos en las comunidades de árboles del bosque nuboso de montaña con relación a los cambios estacionales de temperatura y lluvia (Mendoza et al. 2017). Estos han incluido picos de producción de frutos de la comunidad arbórea en general al final de la estación seca / inicio de la estación húmeda en Costa Rica (Camacho y Orozco 1998) y la Sierra Madre de Chiapas, México (Solórzano et al. 2000), y durante el periodo más húmedo del año en una selva premontana en el Pacífico de Colombia (Hilty 1980). También se han registrado dos picos anuales durante los periodos seco-cálido y húmedo-cálido en Veracruz (Williams-Linera 1997), y de manera similar al final de las estaciones seca y húmeda en Costa Rica (Dinerstein 1986).

Estos patrones de producción de frutos se deben a factores bióticos y abióticos que afectan a las comunidades de árboles o a las historias de vida únicas de las especies individuales que las componen (Van Schaik et al. 1993). Ciertas variables climáticas pueden estar influyendo en los patrones fenológicos de los bosques de montaña, por ejemplo: temperatura, lluvia, radiación solar, vientos extremos, nubosidad o granizo (Wunderle 1999, Bendix et al. 2006, Bustamante et al. 2010, Corredor-Londoño et al. 2020). Los bosques nubosos a menudo tienen cambios estacionales menos drásticos que otros bosques tropicales debido a las altas cantidades de lluvia y cobertura de nubes durante todo el año, y a los cambios de temperatura más moderados (Nadkarni y Solano 2002). Sin embargo, los cambios estacionales en el clima pueden ser evidentes en las elevaciones más altas de los bosques de montaña, especialmente aquellos más alejados del ecuador (Solórzano et al. 2010). Además, los cambios estacionales en la producción de frutos son evidentes incluso en aquellos bosques con baja estacionalidad (Hilty 1980), lo que indica una gama compleja de factores que influyen en estos patrones (Pau et al. 2011, Mendoza et al. 2017).

Influencias bióticas en El Triunfo

Los factores bióticos son generalmente más influyentes en las características de los patrones fenológicos de una comunidad o para una especie dentro de la comunidad, mientras que los factores abióticos son más influyentes en el tiempo en el que ocurren estos patrones (Van Schaik et al. 1993). Los periodos de producción de frutos más cortos, que son bastante constantes en el tiempo entre años, pueden indicar una sincronización con la llegada de algún organismo dispersor de frutos (Mendoza et al. 2017). En El Triunfo, se reportaron dos especies (*Frangula capreifolia*, *Conostegia volcanalis*) que presentaron una producción de frutos en corto tiempo en los 1990s (Solórzano et al. 2000). Sin embargo, otras dos especies que produjeron frutos de mayor tamaño (*Hedyosmum mexicanum*, *Ocotea chiapensis*) tuvieron periodos de producción de frutos más prolongados, lo que indica un periodo de desarrollo más largo que requiere más recursos del árbol (Wheelwright 1986).

Pocas especies produjeron frutos durante los meses más húmedos del año. Dentro de la comunidad de árboles que son recursos alimentarios del quetzal, la especie *Ardisia compressa* produjo frutos durante la mayor parte del año, y no hubo sincronización entre árboles individuales en el momento de la producción.

Esto pudo ser una estrategia para dispersar semillas durante todo el año y evitar la competencia de los dispersores cuando había picos generales en la producción de frutos en el bosque nuboso. Las dos especies de Lauraceae más comunes en el polígono 1 son *Nectandra rudis* y *Ocotea chiapensis*, y su fenología de fructificación podrían haber coevolucionado con el quetzal para producir una gran cantidad de frutos nutritivos durante su periodo reproductivo (Wheelwright 1983).

La producción de frutos en *N. rudis* comenzó cuando los quetzales regresaban a la zona núcleo de polígono 1 desde elevaciones menores u otras áreas del bosque nuboso de El Triunfo, y la producción de *O. chiapensis* fue mayor durante el periodo reproductivo de los quetzales (Solórzano et al. 2000). Estas especies, como otras dentro del área de distribución geográfica del quetzal (Wheelwright 1986), mostraron mayor producción de frutos en un año y menores al siguiente año. Este patrón podría ser una estrategia para alternar la inversión de recursos entre reproducción y crecimiento vegetativo, o también podría depender de los patrones de polinización (Wheelwright 1986).

Las variaciones en los patrones de producción de frutos con relación a los patrones climáticos anuales entre especies también pueden deberse a las variaciones entre especies en el tiempo de desarrollo de los frutos después de la floración (Hilty 1980). En El Triunfo hubo una gran variación en el tiempo entre la floración y la producción de frutos entre especies (Solórzano et al. 2010).

Influencias abióticas en El Triunfo

Los cambios en los patrones fenológicos comunitarios anuales y a largo plazo pueden depender no solo del ciclo de vida, la supervivencia y las interacciones específicas, sino también de las características de los factores abióticos que influyen en cada especie dentro de la comunidad. El tiempo de la producción de flores y frutos de especies con patrones similares cada año puede estar influenciado por factores abióticos que son constantes entre años y durante un periodo de tiempo prolongado, como la duración del día (fotoperiodo) o la radiación solar. Las especies con variaciones de un año a otro en el tiempo de la producción de flores y frutos pueden verse influenciadas por factores climáticos que también pueden variar de un año a otro (Pau et al. 2011), así como por las tendencias a largo plazo (Chapman et al. 2005).

En El Triunfo, dentro de la comunidad de recursos alimentarios del quetzal, diferentes especies arbóreas mostraron patrones que indican posibles influencias de ambos tipos de factores abióticos (constantes y variantes). Por ejemplo, seis especies: *Morus insignis*, *Conostegia volcanalis*, *Citharexylum mocinnii*, *Frangula capreifolia*, *Trophis cuspidata* y *Eugenia capuli* tuvieron patrones fenológicos similares entre 1992 y 1993 en El Triunfo (Solórzano et al. 2000). El tiempo de la producción de frutos en estas especies puede haber sido influenciado por factores abióticos constantes como la radiación solar y la duración del día (Pau et al. 2011), que son mayores durante los meses de verano. No obstante, la cantidad de radiación solar que llega a la superficie del suelo puede verse afectada por la cobertura de nubes (Giambelluca et al. 2011), que a menudo es mayor durante este periodo. Una comunidad arbórea compuesta por estas especies probablemente permanecerá bastante constante en el momento de los patrones fenológicos a largo plazo. Sin embargo, con la inclusión de especies con patrones fenológicos variables, los patrones fenológicos generales de la comunidad también pueden ser variables (Dunham et al. 2018, Pau et al. 2020).

La variación climática es generalmente menor en los bosques nubosos que en los bosques tropicales de menor altitud (Loope y Giambelluca 1998). Sin embargo, en El Triunfo existe estacionalidad en algunas variables climáticas, especialmente las temperaturas mínimas diarias que son más bajas de noviembre a febrero, y las precipitaciones también son bajas durante estos meses y aumentan considerablemente durante el periodo de mayo a octubre (Solórzano et al. 2010). Algunas especies del género *Prunus* requieren un periodo de inactividad, cuando las temperaturas mínimas son más bajas durante el año, para desarrollar flores (Ramírez y Davenport 2016). Esto podría ser una razón de la variabilidad en el tiempo de producción de frutos en *Prunus brachybotrya* entre años en El Triunfo, si las temperaturas mínimas cambian entre años.

La cantidad de lluvia es a menudo el aspecto más variable del clima en los bosques tropicales y ha sido la variable más relacionada con los patrones de producción comunitaria de frutos en estos tipos de bosques (Mendoza et al. 2017). La mayoría de las especies en el bosque nuboso de El Triunfo tuvieron picos en la producción de frutos al final del periodo seco y al inicio del periodo húmedo (Solórzano et al. 2000). Esta puede ser una estrategia para dispersar frutos maduros cuando las condiciones son más favorables para la germinación (McLaren y McDonald 2003). Tres especies: *Nectandra rudis*, *Ocotea chiapensis* y *Trophis cuspidata* desarrollaron sus frutos durante el periodo húmedo y produjeron picos al final de este periodo. *N. rudis* y *O. chiapensis*, pertenecientes a la familia Lauraceae, produjeron frutos más grandes que pueden requerir más disponibilidad de agua para desarrollarse (Chapman et al. 1999). Las tendencias a más largo plazo en la temperatura y en las lluvias en la Sierra Madre pueden provocar cambios en la temporalidad de los patrones fenológicos de la comunidad arbórea debido a los cambios en los patrones de estas especies individuales.

Parte 3. Nicho ecológico del quetzal en El Triunfo

Historia de vida del quetzal

La historia de vida del quetzal tiene una relación importante con los aspectos ecológicos de sus hábitats reproductivos y migratorios. Dentro de su hábitat reproductivo, que se encuentra principalmente en los bosques nubosos de mayor altitud de Mesoamérica (Solórzano et al. 2003), estos aspectos son troncos podridos y árboles que producen frutos nutritivos y accesibles (Ávila et al. 1996, Renner 2005, Carleton y Smith 2016).

Tanto el macho como la hembra buscan un tronco podrido que todavía está en pie y excavan un hoyo en el tronco para construir un nido (Wheelwright 1983). El mismo tronco puede ser reutilizado durante varios años, hasta que éste se pudra demasiado o la cubierta forestal esté disminuida alrededor del tronco (Renner 2005). También es importante para la supervivencia de las crías, la ubicación del tronco en la composición de las especies arbóreas que lo rodean. En Costa Rica, Wheelwright (1983) registró que el tiempo que le tomaba a un padre llevar fruto a sus crías fue de 15 minutos dentro de los primeros 10 días y de seis minutos entre los siguientes 11-21 días. Para obtener recursos suficientes en este tiempo, es necesario que el tronco se ubique cerca de árboles que producen frutos maduros durante el periodo reproductivo de los quetzales, de especies como las de la familia Lauraceae (Ávila et al. 1996), que son altos en lípidos, minerales y proteínas (Carleton y Smith 2016).

Durante el periodo reproductivo del quetzal en El Triunfo, entre enero y junio (Solórzano et al. 2000), la hembra pone dos huevos azules y ambos padres se turnan para incubar los huevos durante 17-18 días. Durante los primeros 6 a 10 días después de la eclosión de los polluelos, se alimentan de proteína animal, principalmente insectos. En los días posteriores, a las crías se les alimenta de una dieta que consiste más en frutos hasta 23 a 30 días después de la eclosión, en los que abandonan el nido (Skutch 1944). También se ha observado que las hembras de quetzales ponen un segundo par de huevos durante la temporada, dos semanas después de que el último polluelo de la primera puesta ha abandonado el nido (Wheelwright 1983). Los quetzales alcanzan la madurez a los 2 años para los machos y a los 3 años para las hembras, y pueden vivir hasta 30 años (Gabriela Santos com. pers.).

Hábitats y migración del quetzal en el polígono 1 de El Triunfo

En El Triunfo, como en otras partes de su distribución (Powell y Bjork 1994), los quetzales suelen migrar altitudinalmente, posiblemente siguiendo la disponibilidad de frutos durante todo el año de diferentes especies arbóreas (Solórzano et al. 2000, obs. pers.). A lo largo de las rutas migratorias en el Polígono 1 (Pineda-Matias 2013), Long y Heath (1991) describieron diferentes comunidades de vegetación, basadas en los árboles o arbustos dominantes. Estas comunidades tuvieron diferentes características que influyeron en la distribución anual de los quetzales en esta área.

La comunidad *Gaultheria-Ugni-Vaccinium* crece en las altitudes mayores de la montaña por encima de los 2100 m donde los vientos son demasiado fuertes para el desarrollo de los árboles, como en la cima del Cerro El Triunfo. En altitudes justo debajo de esta vegetación arbustiva, los árboles más dominantes son *Quercus* sp., y los árboles a menudo tienen un crecimiento atrofiado debido a los fuertes vientos; por ejemplo, el tipo de bosque *Elfin* descrito por Breedlove (1981). En el área de estudio, este bosque se encuentra en los puntos más altos de los senderos Monos, Palo Gordo y Bandera. En estas áreas expuestas hay menor producción de frutos carnosos y pocas de las especies que proporcionan recursos alimentarios para el quetzal crecen en estas áreas (datos no publicados). Estas características topográficas y de la vegetación pueden influir en la separación de las poblaciones locales del quetzal en la Sierra Madre (Pineda-Matias 2013).

Por debajo de las mayores elevaciones de las montañas que rodean el campamento central, en los valles y las cañadas se encuentra la asociación vegetal *Quercus-Matudaea-Hedyosmum-Dendropanax* que se extiende montaña abajo hasta alrededor de 1650 m s.n.m. Este es el principal hábitat reproductivo del quetzal, aunque algunos quetzales pueden reproducirse en bosques de menor altitud en la Sierra Madre si se dispone de troncos podridos y fuentes de alimento (Ismael Gálvez, com. pers.). Este bosque presenta las mejores condiciones para la reproducción debido a la abundancia de especies arbóreas que producen frutos en las zonas más húmedas en las cañadas junto a arroyos y troncos podridos aptos para nidos, como los de la especie arbórea *Heliocarpus donnellsmithii*. Las pendientes orientadas al sur dentro de esta asociación vegetal tienen suelos mejor drenados, más rocosos y más secos. Estas áreas están dominadas por especies de *Quercus*, siendo también común *Symplococarpun purpusii*. Ésta última especie produce frutos al inicio del periodo reproductivo de los quetzales, aunque sin producción constante entre años (Solórzano et al. 2000, obs. pers.).

Una gran parte del área que había sido talada para la agricultura hasta el establecimiento de la reserva en 1990 ahora se ha convertido en un bosque secundario (Castro-Hernández 2019). Este bosque más joven todavía tiene pocos troncos disponibles para nidos y menos especies que producen frutos, aunque especies como *Frangula capreifolia* son más frecuentes en estas áreas y producen frutos maduros al final del periodo reproductivo.

Algunos quetzales permanecen en el hábitat reproductivo de mayor elevación durante todo el año debido a la disponibilidad de frutos de algunas especies como *Ocotea chiapensis*, *Ardisia compressa* y *Trophis cuspidata*, durante el periodo no reproductivo (obs. pers.). Debido a la variabilidad en los periodos de producción de frutos estacionales en individuos de algunas especies de árboles, los frutos están disponibles en diferentes épocas del año, incluso dentro de diferentes partes del bosque nuboso con composiciones de especies similares. Por lo tanto, algunos quetzales pueden migrar a diferentes partes de este bosque durante el periodo no reproductivo y regresar cuando los frutos están en su momento de mayor disponibilidad en la comunidad de árboles con sus recursos alimentarios. Sin embargo, la mayor parte de la población migra altitudinalmente durante la época no reproductiva (Solórzano 1995).

Desde el hábitat reproductivo de mayor elevación, las rutas de migración de los quetzales se encuentran tanto en el lado interior como en el costero de la Sierra Madre (Pineda-Matias 2013). En el lado interior, los bosques son principalmente la comunidad *Liquidambar-Quercus-Pinus*, que tiene algunas de las mismas especies de árboles de recursos alimentarios que el bosque nuboso, como *Podocarpus matudae*, *Trophis cuspidata* y *Ardisia compressa* en las mayores altitudes, y otras especies que proporcionan recursos alimentarios durante el verano, como *Ficus cookii*, en las menores altitudes cercanas a los cafetales. Estas elevaciones más bajas se han fragmentado en gran medida de sus antiguas extensiones de selva tropical, pero todavía contienen árboles que producen frutos en los cafetales de sombra y en áreas ribereñas. También se ha observado que los quetzales consumen frutos de café en algunas áreas de su distribución (García-Rojas 2006).

En la zona costera del Pacífico de la Sierra Madre, existe una gran diversidad de árboles que producen frutos consumidos por el quetzal de las comunidades *Ficus-Coccoloba-Dipholis-Sapium* (1200-1600 m s.n.m.) y *Garcinia-Inga-Desmopsis* por debajo de los 1200 m s.n.m. (Solórzano 1995). Estas comunidades incluyen especies que producen frutos durante todo el año (Ragusa-Netto 2002) y posiblemente durante el verano, cuando hay escasez de frutos en las mayores elevaciones.

El nicho ecológico eltoniano del quetzal

Generalmente, el nicho ecológico de una especie incluye los aspectos climatológicos y ecológicos necesarios para su supervivencia. La gran variedad climática de los hábitats reproductivos y migratorios del quetzal en la Sierra Madre indican que sus tolerancias climáticas dentro de los extremos altitudinales de su migración son probablemente mayores que las de los árboles que producen sus recursos alimentarios. Por lo tanto, las características del nicho ecológico del quetzal están más influenciadas por los factores ecológicos de su hábitat, especialmente los patrones de producción de frutos de sus recursos alimentarios. Estos patrones pueden determinar el momento de la migración y el regreso al hábitat reproductivo y el periodo de reproducción. Estas características del ambiente que se requieren para que una especie sobreviva encajan en la definición del nicho ecológico eltoniano de una especie (Peterson et al. 2011).

Con base en observaciones de quetzales en Costa Rica, Wheelwright (1983) sugirió que la migración del quetzal puede depender de la disponibilidad de frutos de la familia Lauraceae, ya que producen frutos ricos en nutrientes importantes para los polluelos (Ávila et al. 1996, Carleton y Smith 2016). En El Triunfo, Solórzano et al. (2000) determinaron que la abundancia de quetzales se correlacionó con el número de especies productoras de frutos y el número total de frutos producidos en la comunidad de sus recursos alimentarios, pero no específicamente con frutos de la familia Lauraceae. La abundancia de quetzales también se ha relacionado con la abundancia de sus recursos alimentarios a diferentes altitudes en Guatemala (Bustamante et al. 2010). Más recientemente en Costa Rica, García-Rojas (2006) observó quetzales en las mayores elevaciones cuando había más especies que producían frutos, pero durante el mismo periodo, había un mayor número de especies que producían frutos en los bosques de menor elevación.

Entre las observaciones de Solórzano et al. (2000) en 1991-1993 y las observaciones recientes realizadas como parte del monitoreo de especies prioritarias por CONANP de 2010-2020, hubo una disminución general en el número de quetzales observados durante el pico de su periodo reproductivo de febrero a abril. Sin embargo, la población posiblemente más pequeña de quetzales en el polígono 1 parece permanecer en su hábitat reproductivo durante un periodo de tiempo más largo antes de migrar y regresar a este hábitat antes de la fecha que se reportó a principios de la década de 1990 (CONANP 2020). Si la relación entre la abundancia del quetzal y sus recursos alimentarios ha continuado, esto puede indicar que los patrones fenológicos de los árboles pueden haber cambiado desde que se hicieron las observaciones en la década de 1990.

PREGUNTAS DE INVESTIGACIÓN

1. ¿Se han producido tendencias significativas (de 27 años) en la temperatura y las lluvias desde 1990 en la Sierra Madre, y cómo se han relacionado estas tendencias con los cambios en las influencias climáticas regionales y a gran escala (atmosférica y oceánica)?

2. ¿Existe correlación entre las variables climáticas y la producción de flores y frutos en las especies arbóreas que producen los recursos alimentarios del quetzal en el bosque nuboso de El Triunfo, y han cambiado estos patrones entre 1992-1993 y 2019-2021?

3. ¿Existe un patrón espacial (relacionado con la composición del bosque) o temporal (relacionado con la producción de frutos) en la abundancia de quetzales en el bosque nuboso de El Triunfo?

HIPÓTESIS

1. **Razonamiento**: Los cambios a gran escala que influyen en el clima de la región del Pacífico de Chiapas, incluyendo los atmosféricos (aumentos en los niveles de CO_2; Liverman y O'Brien 1991) y oceánicos (tendencia decreciente en el índice de la Oscilación Decadal del Pacífico, aumento de la temperatura de la superficie del mar en el Golfo de México y el Caribe; Méndez-González et al. 2010, Lluch-Cota et al. 2013) han ocurrido desde 1990. Las tendencias decrecientes en la deforestación, las condiciones sociales y económicas cambiantes y el establecimiento de reservas de biosfera (Cano-Díaz et al. 2015, Bonilla-Moheno y Aide 2020) indican que también pueden haber ocurrido cambios en la cobertura vegetal regional, lo que posiblemente influye en las características de precipitación orográfica de la Sierra Madre (Lawton et al. 2001, Barradas et al. 2010).

   Hipótesis: El clima de la Sierra Madre y áreas adyacentes de menor elevación de la región del Pacífico de Chiapas ha estado cambiando desde 1990. Existe una relación entre las tendencias climáticas en esta región y los cambios en las influencias climáticas a gran escala (atmosférica y oceánica) y regionales (vegetación).

2. **Razonamiento**: Las especies de árboles con variaciones en sus patrones fenológicos entre años pueden verse influenciadas por factores climáticos más variables como la temperatura y las lluvias (Van Schaik et al. 1993, Pau et al. 2011). Los patrones de producción de frutos han ido cambiando en los bosques tropicales a medida que los patrones de temperatura y lluvia han ido cambiando o se han registrado tendencias a largo plazo (Chapman et al. 2005, Barnes 2015, Dunham et al. 2018).

Hipótesis: Existe una relación entre el clima y la producción de flores y frutos, especialmente en aquellas especies arbóreas con patrones anuales variables. Las tendencias de ~30 años en la temperatura y la lluvia influirán en los cambios en los patrones fenológicos de ciertas especies de árboles, por lo tanto, repercutirán en los patrones fenológicos de la comunidad general de los recursos alimentarios del quetzal entre 1992-1993 y 2019-2021.

3. **Razonamiento**: Desde el establecimiento de la Reserva de la Biosfera El Triunfo en 1990, las áreas de cobertura forestal han aumentado dentro de la zona núcleo del polígono 1. Esto ha incrementado potencialmente el hábitat y la abundancia de recursos alimentarios para el quetzal en esta área. La ausencia de perturbaciones en la zona núcleo indica que las especies arbóreas que proporcionan recursos alimentarios al quetzal continúan presentes. La relación entre la abundancia del quetzal y los frutos del bosque nuboso se ha observado en Costa Rica (Wheelwright 1983, García-Rojas 2006), Guatemala (Bustamante et al. 2010) y El Triunfo (Solórzano et al. 2000). Los cambios en la disponibilidad de recursos alimentarios también han afectado la abundancia de especies de aves en otros bosques tropicales de América (Lister y García 2018).

   Hipótesis: Continuará existiendo una relación en 2019-2021 entre la abundancia de quetzales y la producción de frutos que consumen en el bosque nuboso de El Triunfo, como se documentó en 1992-1993. Si los patrones fenológicos de los recursos alimentarios han cambiado, esto influirá en la abundancia mensual de quetzales en su hábitat reproductivo. Los quetzales serán más abundantes en los tipos de bosques con una mayor diversidad de especies arbóreas productoras de recursos alimentarios durante las épocas de mayor producción de biomasa.

OBJETIVO GENERAL

Determinar si las tendencias climáticas desde 1990 en la Sierra Madre están afectando los patrones fenológicos de los recursos alimentarios y la abundancia del quetzal en su hábitat reproductivo del bosque nuboso de El Triunfo.

OBJETIVOS ESPECÍFICOS

1. Evaluar posibles cambios de temperatura y lluvia en la Sierra Madre de Chiapas en el periodo 1990-2016 y su ubicación, e inferir cómo los factores regionales y de gran escala (atmosférica y oceánica) pueden haber influido en estos cambios.

2. Determinar si existe relación entre las variables climáticas y los patrones fenológicos en especies arbóreas del bosque nuboso de El Triunfo, y si estos patrones han cambiado entre 1992-1993 y 2019-2021.

3. Determinar los patrones de abundancia anual del quetzal en su hábitat reproductivo del bosque nuboso de El Triunfo, y si estos patrones están relacionados espacialmente y temporalmente con la abundancia de los frutos como su recurso alimentario.

5. ÁREA DE ESTUDIO

Este estudio se centró en los cambios climáticos y ecológicos en la cordillera de la Sierra Madre de Chiapas (en adelante, Sierra Madre) en dos escalas espaciales. El análisis de tendencias climáticas (Capítulo 2) incluyó esta región montañosa y las dos regiones fisiográficas adyacentes, la Depresión Central y las llanuras costeras del Pacífico (Costa) (Figura 1). Estas tres regiones fueron denominadas "Pacífico Chiapas" en este capítulo. Las observaciones de campo de la fenología de árboles (Capítulo 3) y la abundancia de quetzal (Capítulo 4) se realizaron en una parte de la Sierra Madre ubicada dentro del bosque nuboso (Breedlove 1981) de la Reserva de la Biosfera El Triunfo (Figura 2).

El análisis de las tendencias de temperatura y de lluvia, e influencias regionales sobre el clima de la Sierra Madre se realizó con datos climáticos recolectados por las estaciones climáticas en la región Pacifico Chiapas entre el periodo de 1960 y/o 1990 hasta 2016 (Capítulo 2). La compleja topografía y la posición de esta región entre tres cuerpos de agua principales: Océano Pacífico, Golfo de México y Mar Caribe, crean las condiciones para el crecimiento de una amplia gama de tipos de vegetación.

Los tipos de vegetación en la región de la Costa incluyen manglares, matorrales costeros, humedales y palmeras, agricultura (principalmente plátanos, árboles frutales, aceite de palma y caña de azúcar) y algunos remanentes de selva tropical. Para la Sierra Madre los tipos de vegetación incluyen selva tropical en las laderas del Pacífico inferior, plantaciones de café de sombra, bosques de pino-encino, bosques nubosos y pequeñas áreas de bosques de *Abies* y cipreses en las mayores elevaciones. En la parte más baja del interior de la Sierra Madre, los tipos de vegetación incluyen bosques de pino-encino-liquidámbar, bosques tropicales húmedos y caducifolios, y vegetación de matorrales (INEGI 2017). La región de la Depresión Central estuvo una vez cubierta principalmente por bosques tropicales caducifolios, pero gran parte de estos se han talado para la agricultura (Vaca et al. 2012).

Entre 1970 y 1990 hubo una gran cantidad de cambios en el uso del suelo en esta área, principalmente deforestación (Richter 2000, Solórzano et al. 2003). Sin embargo, desde 1990, el establecimiento de reservas de la biosfera en la Sierra Madre y las cambiantes condiciones sociales y económicas (Cano-Díaz et al. 2015), así como las tendencias decrecientes en la deforestación o restauración en partes de Centroamérica (Fagan et al. 2013), indican que entre 1990 a 2020 también pudo haber sido una época de cambio en el uso del suelo. Las posibles implicaciones climáticas de estos cambios regionales (vegetación y evapotranspiración) fueron analizadas en el presente trabajo entre los años 1990 y 2020.

También se discutieron los cambios en las condiciones oceánicas y atmosféricas a mayor escala que influyen en el clima de la región del Pacífico sur de México, con relación a las tendencias de temperatura y de lluvia en la Sierra Madre. Las relaciones entre estas tendencias climáticas y patrones fenológicos de los recursos alimentarios del quetzal en la Sierra Madre se realizaron utilizando los datos recolectados durante el trabajo de campo de este proyecto.

Las observaciones de patrones fenológicos (producción de flores y frutos) de árboles productores de recursos alimentarios (Capítulo 3), parcelas de árboles de recursos alimentarios y observaciones de abundancia de quetzal (Capítulo 4), se realizaron en el bosque nuboso de la zona núcleo del polígono 1 de la Reserva de la Biosfera El Triunfo (El Triunfo) (Figura 2). Este es un sitio reproductivo importante del quetzal y otras especies como el tucán (*Aulacorynchus prasinus*), el mono araña (*Ateles geoffroyi*), la ardilla (*Sciurus* sp.) y el pavón (*Oreophasis derbianus*), que consumen las mismas especies de frutos que el quetzal (González-García et al. 2017). Esta área se encuentra principalmente en un valle protegido que presenta una comunidad de vegetación de *Quercus-Matudaea-Hedyosmum-Dendropanax* (Long y Heath 1991).

El estudio de campo se centró en la zona núcleo del polígono 1 para que las observaciones de la fenología de frutos de los años 2019-2021 pudieran compararse con los datos recopilados en 1992-1993 (Solórzano et al. 2000). Los patrones de abundancia local y estacional de quetzal a más largo plazo también podrían analizarse en esta área debido a la disponibilidad de datos mensuales recopilados desde enero de 2010 durante el programa de monitoreo de especies prioritarias. Esta es una de las áreas más conservadas en El Triunfo, y los estudios de los patrones fenológicos de los árboles y las relaciones con la abundancia del quetzal pueden usarse para planificar la restauración ecológica del hábitat del quetzal y otros frugívoros en áreas de la Sierra Madre que han sido dañadas o degradadas.

En el polígono 1 de El Triunfo hay seis senderos donde se hicieron las observaciones fenológicas y de quetzales: Cerro El Triunfo, Palo Gordo, Bandera, Finca Prusia, Costa y Monos (Figura 2). Las áreas de mayor elevación se encuentran en los senderos Cerro El Triunfo, Palo Gordo, Bandera y Monos por encima de los 2100 m s.n.m., a menudo están expuestas a fuertes vientos y están más dominadas por especies de encinos. Las mayores elevaciones del sendero Cerro El Triunfo están dominadas por arbustos debido a las condiciones expuestas. El sendero Costa comienza en una cañada y viaja hasta la vertiente del Pacífico donde los vientos son más fuertes, y de esta vertiente hasta el bosque de cipreses. Debajo de los bosques de cipreses, comienza la vegetación de selva mediana perennifolia que produce frutos importantes para el quetzal durante su periodo migratorio (Solórzano et al. 2000).

El clima de la zona núcleo del polígono 1 es más estacional para temperaturas mínimas (nocturnas) y lluvias. Las temperaturas mínimas diarias son más bajas durante los meses de diciembre, enero y febrero (en la década de 1990 era de aproximadamente los 0 ^{o}C) y aumentaban ~10 ^{o}C en mayo-octubre. Las temperaturas máximas oscilaban entre los 23 ^{o}C en enero y los 25 ^{o}C en mayo. Las precipitaciones son bajas en los meses de noviembre a abril y máximas en los meses de mayo a octubre (~500 mm/mes), con ~700 mm/mes durante el periodo de tormentas en septiembre. Entre 1990 y 2020, los principales cambios climáticos en esta zona de la Sierra Madre fueron el aumento de las temperaturas mínimas diarias, un inicio más temprano de la temporada de lluvias y un aumento de las lluvias durante este periodo.

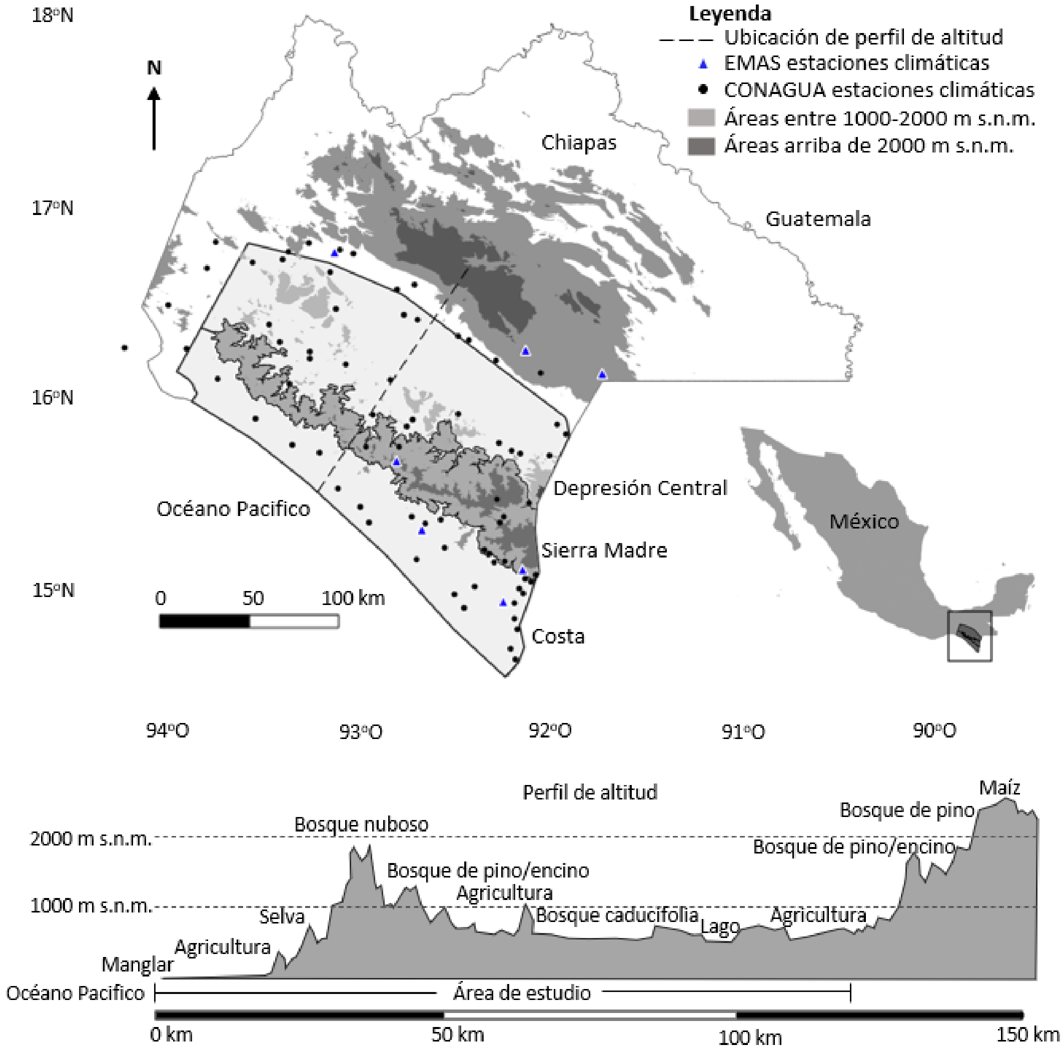

Figura 1. Área de estudio del Capítulo 2 en las tres regiones fisiográficas de Chiapas más cercanas al Océano Pacifico: el Depresión Central, Sierra Madre y Costa.

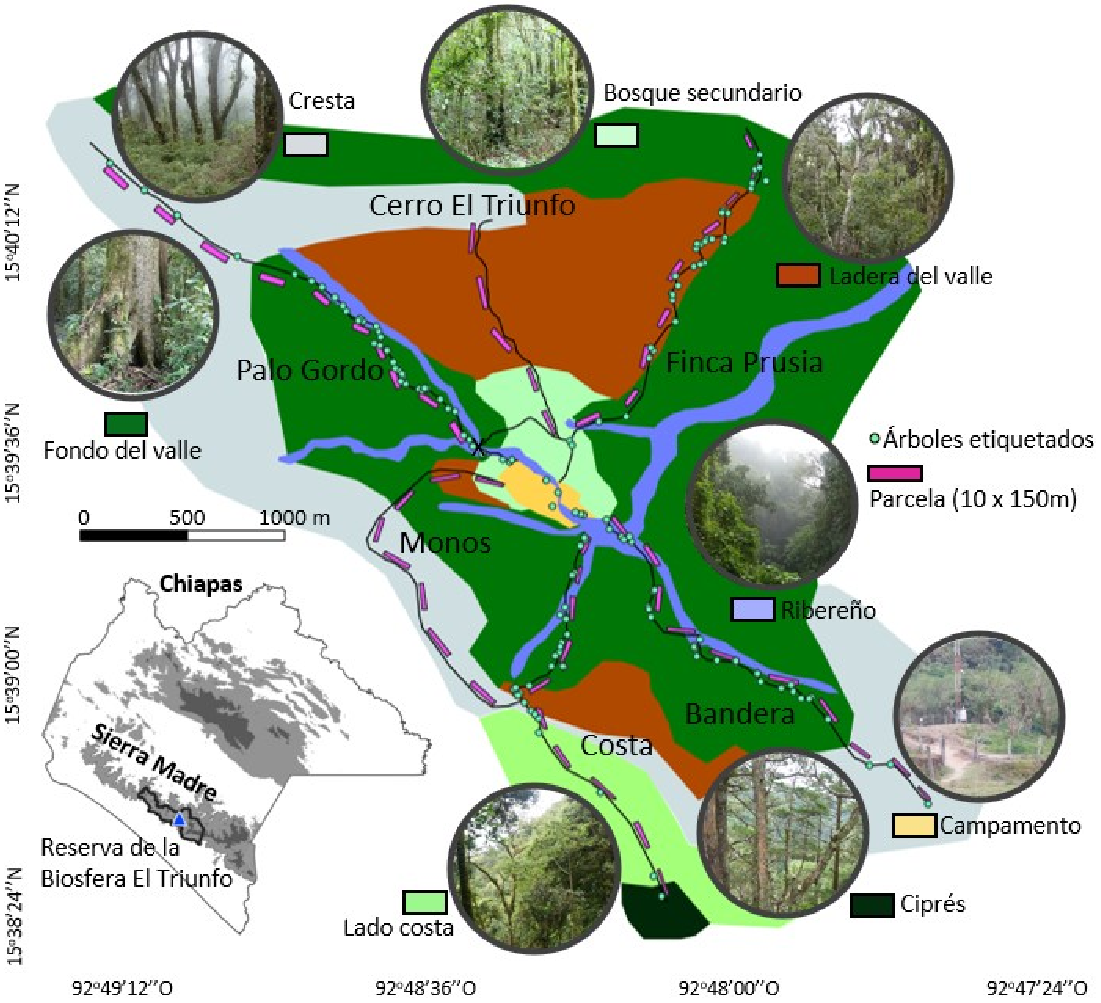

Figura 2. Área de estudio de los Capítulos 3 y 4 en la zona núcleo del polígono 1 de la Reserva de la Biosfera El Triunfo, Chiapas, México.

CAPÍTULO 2

Vertiente del pacifico, Reserva de la Biosfera El Triunfo. Foto de Allen Wootton.

Regional patterns of vegetation, temperature, and rainfall trends in the coastal mountain range of Chiapas, Mexico*

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*Artículo publicado en Atmósfera.

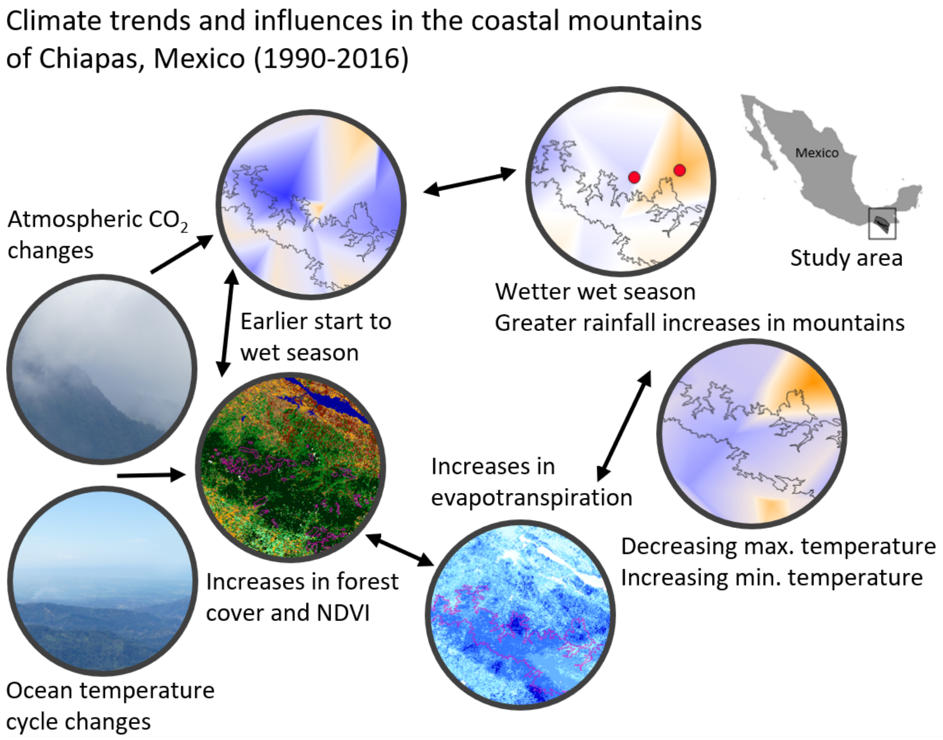
Wootton, A., Enríquez, P.L., & Navarrete-Gutiérrez, D. 2021. Regional patterns of vegetation, temperature, and rainfall trends in the coastal mountain range of Chiapas, Mexico. Atmósfera. (Early online release) https://doi.org/10.20937/ATM.53026.

Climate trends and influences in the Sierra Madre de Chiapas

HIGHLIGHTS

- Increases in regional NDVI, evapotranspiration, and rainfall in mountains
- Greater rainfall increases in mountains than at lower elevations
- Range between min and max temperature decreased in Pacific Chiapas
- Variable directions in local temperature and rainfall trends within regions
- Variable directions in temperature trends between 1960-1989 and 1990-2016

GRAPHICAL ABSTRACT



Climate trends and influences in the coastal mountains of Chiapas, Mexico (1990-2016)

RESUMEN

Los cambios en el CO_2 atmosférico, la temperatura del océano y las condiciones de la vegetación regional en Mesoamérica indican que podrían haber ocurrido tendencias significativas en la temperatura y las lluvias en la Sierra Madre de Chiapas, México. Esta es una región importante para la flora y la fauna que podría verse afectada por las tendencias climáticas. Nuestro objetivo fue determinar si y dónde se habían producido tendencias climáticas en 27 años en la Sierra Madre y las regiones de menor elevación entre 1990-2016, si estas tendencias eran parte de cambios a más largo plazo de 1960-2016 (57 años), y cómo los cambios en las condiciones de gran escala y regionales/locales pueden estar influyendo en estas tendencias. En la Sierra Madre, las temperaturas diarias mínimas generales aumentaron, las temperaturas máximas disminuyeron y la mayoría de las tendencias significativas de temperatura media fueron más frías durante el periodo de 27 años. Tanto el inicio como el final de la temporada húmeda mostraron una tendencia a principios de año, y las lluvias de esta temporada aumentaron significativamente. Las tendencias no fueron significativas durante el periodo de 57 años en la Sierra Madre; sin embargo, en la región adyacente de la costa del Pacífico, continuaron las tendencias significativas de temperaturas más cálidas durante este periodo. Dentro de las regiones, hubo una gran variación en los cambios de temperatura y precipitación, y algunas tendencias locales fueron opuestas a los promedios regionales. Los procesos a gran escala de calentamiento de las temperaturas de la superficie del mar en la costa este de México, un cambio de la fase positiva a negativa de la Oscilación Decadal del Pacífico y los aumentos en el CO_2 atmosférico pueden estar influyendo en estas tendencias. A escala regional, los aumentos en la vegetación densa y la evapotranspiración desde 1990 pueden haber creado características que favorecen una retroalimentación positiva de una mayor humedad oceánica y un ciclo de precipitación basado en la vegetación.

Palabras claves: Cambios de vegetación, evapotranspiración, percepción remota, Sierra Madre, tendencias climáticas

ABSTRACT

Changes in atmospheric CO_2, ocean temperature, and regional vegetation conditions in Mesoamerica indicate that significant trends in temperature and rainfall may have occurred in the Sierra Madre de Chiapas, Mexico. This is an important region for flora and fauna which could be affected by climate trends. We aimed to determine if and where (27-year) climate trends had occurred in the Sierra Madre and lower elevation regions between 1990-2016, if these trends were part of longer term 1960-2016 (57-year) changes, and how changes in large-scale and regional/local conditions may be influencing these trends. In the Sierra Madre, overall minimum daily temperatures increased, maximum temperatures decreased, and most significant mean temperature trends were cooler during the 27-year period. Both the start and end of the wet season trended earlier in the year, and wet season rainfall increased significantly. Trends were not significant during the 57-year period in the Sierra Madre; however, in the adjacent Pacific coast region, significant warmer temperature trends continued during this period. Within regions, there was large variation in temperature and rainfall changes and some local trends were opposite to the regional averages. Large-scale processes of warming sea surface temperatures in the east coast of Mexico, a change from the positive to negative phase of the Pacific Decadal Oscillation, and increases in atmospheric CO_2 may be influencing these trends. At the regional scale, increases in dense vegetation and evapotranspiration since 1990 may have created characteristics favoring a positive feedback of higher ocean-based moisture and vegetation-based precipitation cycling.

Key words: Climate trends, evapotranspiration, remote sensing, Sierra Madre, vegetation changes

1. Introduction

Changes since 1990 in influences to the climate of Mesoamerica, including atmospheric (Liverman and O'Brien, 1991; NOAA, 2020a), ocean temperature (Méndez-González et al., 2010) and land cover (Bray, 2009), indicate that significant regional climate trends may have occurred. Predictions or explanations of the causes of climate trends or changes in these regions has often been done based on modelling of global atmospheric conditions (Karmalkar et al., 2008), ocean temperature patterns (Pounds et al., 1999), or regional land use changes (Ray et al., 2006a; Barradas et al., 2010). However, as each tropical region has its own particular topographical, oceanic influence and land cover change circumstances, the use of local data is also necessary to determine spatial detail in actual regional trends and validate models.

The three physiographical regions of the Mexican state of Chiapas closest to the Pacific Ocean (subsequently referred to as Pacific Chiapas) are the Central Depression, Pacific coastal plains (Coast) and Sierra Madre de Chiapas (Sierra Madre) (Fig. 1). The climate of this area is largely influenced by large scale circulation patterns, which determine the direction of airflow, onset and length of the wet season, and frequency and intensity of rainfall events (Hewitson and Crane, 1992). The influence on regional climates of these large-scale processes may depend on trends in sea surface temperatures (SST) (Aguilar et al., 2005), which have been increasing in the Gulf of Mexico and Caribbean Sea since 1965 and 1975 respectively, in the regions closest to the east coast of Mexico (Lluch-Cota et al., 2013).

Short term variation in temperature and precipitation patterns in Chiapas have been found to be weakly correlated with cycles of El Niño Southern Oscillation in the Pacific Ocean, although regional climate patterns varied in relation to this phenomenon (Golicher et al., 2006). Changes between the positive and negative phase of the Pacific Decadal Oscillation (PDO) could also affect climate trends during a longer time period (Méndez-González et al., 2010).

In addition to ocean temperature trends, changes in amounts of atmospheric CO_2 may be influencing the climate of the region. Based on CO_2 modelling, Liverman and O'Brien (1991) predicted that if CO_2 doubled from the 1990 amount of 350 ppm, this would cause increases in air temperature and late dry season and summer precipitation, and decreases in precipitation at the end of the wet season and beginning of the dry season in parts of Chiapas. Since this time, atmospheric CO_2 has increased to 415 ppm in 2020 (NOAA, 2020a).

Regional changes to land vegetation characteristics within Pacific Chiapas may also be influencing the mountain climate of the Sierra Madre. Modelling done on the effect of forest cover change on cloud formation in Costa Rica found that scenarios with large amounts of lower elevation deforestation resulted in lower amounts of cloud cover and higher base cloud heights in mountain forests (Lawton et al., 2001; Ray et al., 2006a). These climatic changes were largely attributed to increases in sensible heat flux from cleared land and reductions in latent heat flux due to vegetation losses (Lawton et al., 2001; Ray et al., 2006a).

Forests and dense vegetation contribute large amounts of water vapour to the atmosphere through evapotranspiration (ET), and can affect regional rainfall through recycling of ocean source moisture (Durán-Quesada et al., 2012). Changes in vegetation can affect this process (Sheil, 2018), with reductions in tropical forest cover generally leading to reductions in regional rainfall (Chambers and Artaxo, 2017; Casagrande et al., 2018). The main factors which control ET in an environment are vegetation density and leaf production, and climatic variables such as temperature, irradiance, wind, soil water availability, and vapour pressure (Zhang et al., 2015). In regions which are mainly covered in vegetation, such as the study area, the process of transpiration contributes to the greatest portion of ET (Ramón-Reinozo et al., 2019), although evaporation from leaf surfaces can contribute to a significant portion (Ballinas et al., 2015). In a watershed in the Sierra Madre, Castro-Mendoza et al. (2016) estimated that up to 64% of precipitation may be re-cycled to the atmosphere through ET.

Changes in vegetation cover may also affect local trends in temperature and rainfall, however the effects of this in tropical regions is still unclear. In the Lacandon rainforest in eastern Chiapas, maximum daily temperatures generally decreased in areas where there had been deforestation, but there was no relation between local rainfall and forest cover changes (O'Brien, 1998). In Guatemala, areas with greater deforestation within similar forest types had lower amounts of rainfall during the dry season (Ray et al., 2006b). The determination of links between vegetation changes and climate trends are especially important in tropical regions such as Chiapas where land use change has been occurring rapidly (Solórzano et al., 2003).

These measured or potential changes in oceanic, atmospheric, and regional land cover conditions, indicate the potential for climatic change in Pacific Chiapas. Therefore, this study examines the actual effects of these changes in large-scale and regional climatic influences on temperature and rainfall trends in this area, especially the Sierra Madre mountain range, from 1990 to 2016.

The Sierra Madre is the main source of water which flows into the Grijalva River system to produce a large quantity of Mexico’s power from dams, and is an important source of freshwater resources (Jones et al., 2018). It is also a major coffee producing region, which may be affected by changes in climate (Schroth et al., 2009). Its ecological importance has been recognized through the establishment of the biosphere reserves: El Triunfo, La Sepultura and Volcán Tacaná. These reserves contain populations of flora and fauna which may be affected by long term changes (Rojas-Soto et al., 2012), or cyclical (~30-year) trends in the mountain climate (Pounds et al., 1999; Lister and Garcia, 2018). Various ecological studies were conducted during the establishment the reserves in the early 1990’s (e.g., Long and Heath, 1991; Solórzano et al., 2000), and a better understanding of climatic trends since 1990 may provide a useful reference to help explain longer term ecological trends in this region (González-García et al., 2017).

The aims of the study were to determine if and where significant climate trends have occurred from 1990-2016 in Pacific Chiapas, if these were cyclical (~30 year) trends or part of longer-term (~60 year) climate changes, and how regional and larger scale processes may be influencing these trends or changes. Specifically, the first objective was to determine spatial patterns of temperature and rainfall changes and locations of significant trends from 1990-2016 in the Sierra Madre to compare with those of the adjacent lowland regions. The second objective was to determine if significant trends during the 27-year period were part of a longer-term (1960-2016) trend in locations where data were available. The third objective was to relate climate trends to larger scale and regional climatic influence changes during similar time periods.

As mentioned, various studies have described how large scale oceanic (Hewitson and Crane, 1992) and atmospheric processes (Liverman and O'Brien, 1991) may influence the climate of Pacific Chiapas, and we incorporated these findings into the discussion of the determined climate trends. However, to our knowledge, there have been no previous studies which have included vegetation characteristics and changes in relation to climate trends in this region. Therefore, the third objective focused on the determination of local and regional changes in vegetation and ET from 1990-2020 which may also be influencing climate trends in Pacific Chiapas, and in particular the mountain regions.

2. Methods

2.1 Study area and time period

Pacific Chiapas (Fig. 1) is a topographically and ecologically complex region where mountainous and coastal terrain create conditions for the growth of many different forest types including mangroves, rainforests, tropical deciduous, oak-pine, cypress, fir, and cloud forests (INEGI, 2017; Fig. 1). Leaf presence is especially seasonal in the tropical deciduous forests (Gómez-Mendoza et al., 2008), but also in the more evergreen mountain forests where ET can change greatly throughout the year (Ballinas et al., 2015).

Similar to other regions of southern Mexico, the majority of rainfall falls between June and September (Brito-Castillo, 2012). The timing of the onset of the wet season depends strongly on the northward movement of the Intertropical Convergence Zone (ITCZ), which causes trade winds to increase in intensity and bring moist air from the Caribbean and Gulf of Mexico (Brito-Castillo, 2012). During the summer and early fall, tropical cyclones originating from the Caribbean Sea and Pacific Ocean, can bring large amounts of rainfall (García, 1974). Winter rainfall is less and is affected by cold winds originating in central North America which travel over the Gulf of Mexico, collecting humidity (García, 1974). Low pressure systems in northern Mexico also bring in moist air from Pacific during the winter (Brito-Castillo, 2012). Amounts of yearly rainfall (1990-2016 averages) are greatest in the Sierra Madre (Finca A. Prusia weather station: 2860 mm/year, with 85% of rainfall during the wet period from June until October), followed by the Coast (Tapachula: 2076 mm/year, 78% during the wet period), and lower amounts in the Central Depression (Villaflores: 1222 mm/year, 86% during the wet period) (Fig. 2).

Daytime (maximum) temperatures are highest in this region just before the wet season due to higher latent heat transfer and radiative forcing (Aguilar et al., 2005). July is often the month with the highest nighttime (minimum) temperatures due to the insulation caused by higher cloud cover (Aguilar et al., 2005). Mean daily temperatures (1990-2016 averages) are highest in the Coast (Tapachula: 29 ºC), and lower at higher elevations in the Central Depression (Villaflores: 24 ºC), and the Sierra Madre (Finca A. Prusia: 22 ºC) (Fig. 2). In addition to ocean moisture sources, temperature and rainfall patterns in Pacific Chiapas are also influenced by topography and vegetation characteristics (Hewitson and Crane, 1994; Ray et al., 2006b).

Analysis of data began with the year 1990 to include greater spatial detail of climate trends with the inclusion of larger numbers of weather stations which began collecting data around this year; and to provide a climatic reference to compare ecological changes in the Sierra Madre. Comparisons of 1990-2016 trends were also done for a longer-term (57 year) period using data from weather stations where significant 1990-2016 trends were determined and data were available since 1960.

Temperature and rainfall data were obtained from Comisión Nacional del Agua (CONAGUA, 2018) weather stations located within the study area (Fig. 1, SM Table I in supplementary material). Because of a lack of complete data in some weather stations and years with large amounts of cloud cover in Landsat satellite images, the analysis of land cover, NDVI, and potential ET was done using data from a range of years. Satellite images from 1987-1993 were used to represent the year 1990 and images and data from 2015-2020 to represent 2020. Rainfall and temperature trend analysis was done from the period of 1990-2016 for most stations, or to 2012 or 2015 where more recent data were not available (SM Table VII).

2.2 Temperature and rainfall trends

Trends and changes in average minimum (Tmin), mean (Tmean), and maximum (Tmax) daily temperature between 1990-2016 were determined using data from 55 weather stations located within the study area (SM Table I). Months were grouped into three seasons representing the main yearly changes in temperature: dry-cool (November-February), dry-hot (March-May), and wet (June-October). Temperature data for each season were obtained by averaging data of the months within each group. Differences in temperature were generally greater between months within a season than between adjacent years of the same month. Therefore, if a month was missing data, they were estimated by calculating the average of the closest years (for up to one or two years) where data were available. This was done to avoid cooler or warmer month biases within the seasonal monthly averages where some monthly data were missing. If a station was missing more than 15% of monthly data between 1990-2016, or errors were evident (e.g., sudden breaks between temperature trend lines), it was not included in the analysis.

A graph of the temperature data was done for each month for each weather station and a least squares regression line was applied from the year 1990 to 2016. The average daily temperature value of the regression line value in 2016 was subtracted from that of 1990 to determine the change between these years. These data were uploaded into the GIS software QGIS version 3.14, as vector points and a spatial analysis of temperature changes was done using the Triangulated Irregular Network (TIN) method (Mitas and Mitasova, 1999) in QGIS for each season. This was chosen as the method to best represent the interpolation of the spatial changes in the data which were largely influenced by topography (Velasquez et al., 2011).

Using climatic records with gaps in time series creates some uncertainty when assessing trends (Mardero et al., 2019). To correct for this, Mardero et al. (2019) interpolated data from near-by weather stations in the low elevation Yucatan Peninsula to complete rainfall records. Interpolation was also attempted in our study for stations in the Sierra Madre with missing data or years without data from 2012-2016 (SM Table VII). However, results of this interpolation were inaccurate due to the large variation in rainfall between stations in the topographically complex mountain range. Therefore, the analysis of rainfall trends was done using only available data (SM Table V, SM Table VII).

Monthly rainfall changes between 1990-2016 were determined using the same method to calculate temperature changes, with data from 76 weather stations. Significant trends ($p<0.05$) in temperature and rainfall were determined for three periods: 1960-1989, 1960-2016 and 1990-2016 (where data was available) using the Mann-Kendall test in the excel extension program XLSTAT 2019. This test has commonly been used to detect significant trends in climate data. It has the assumption that data records are independent, but these data do not need to be normally distributed. As it is non-parametric, results of the test are not influenced by outlier values (Ahmad et al., 2015). Another advantage of using the Mann-

Kendall test is that trends can still be determined even if a time series has missing data.

The start, end, and length of the wet season was calculated locally (rather than with regional averages) using daily rainfall data from 65 weather stations. Specifications of the start of the wet season were modified from a similar study done for the Yucatan Peninsula (Mardero et al., 2019). These were: (1) the first day of the year with measurable rainfall (≥1mm) followed by at least another day of rainfall within the next five days for a total of at least 20 mm of rainfall; and (2) that within the 30 days following this first day of rainfall, there was no dry spell of seven or more consecutive days without rainfall. The end of the wet season was calculated using these specifications in reverse, and the length of the wet season was calculated as the number of days between the start and the end of the wet season. Changes in the start and end of the wet season were determined by applying a regression line to a graph of the start and end dates and subtracting the values at the years 2016 and 1990 from the regression line.

2.3 Vegetation classification

Analysis of the spatial extent of forest and other vegetation cover in the years 1990 and 2020 was done to determine vegetation changes which could partially explain changes in ET, temperature, and rainfall in the study time period. The spatial extent of vegetation types was determined within the study area from the classification of Landsat Level-2 atmospherically corrected images (SM Table II). Classification was done from images captured during the dry season in order to determine vegetation types based on their density and leaf seasonality characteristics which could affect seasonal ET (Glenn et al., 2011; Ballinas et al., 2015). Images covering the study area, captured during 1987-1993 (Landsat 5) and 2017-2020 (Landsat 8) and which had less than 10% cloud cover, were downloaded from the USGS Earth Explorer website (USGS, 2020). The green, red and infrared bands (bands 2, 3, and 4 of Landsat 5, and bands 3, 4, and 5 of

Landsat 8) were combined in QGIS, and these resulting images were uploaded into the land classification software program Multispec Application, version 3.4.

Supervised classification of the image was done in this program to determine the land cover classes: evergreen forest (primary and secondary coniferous, cloud, and rainforest), mangrove, palm plantations, semi-deciduous forest (oak, pine-oak, fruit tree), deciduous forest, scrub, irrigated agriculture or short vegetation (often wetlands), grassland or seasonal agriculture, areas without vegetation (bare soil, rock, urban areas), water (lakes, rivers, coastal waters within the study area), and cloud cover (Table I). Evergreen forest, mangroves and palm plantations were determined as separate classes for areas dominated with tree cover which appeared as darker red in the combination of satellite images. As these evergreen forest types had similar spectral characteristics, images covering the coast and coastal plains were classified separately from the mountain and inland areas to not erroneously classify mangroves or palm plantations within the entire study area.

Semi-deciduous forest appeared as a fainter dark red, deciduous forest as darker brown and scrub as lighter brown. Irrigated agriculture or wetlands appeared as lighter red or darker pink, and non-irrigated fields or soil as light grey (Fig. 3). Coastal wetland and coffee plantation subclasses were difficult to distinguish from the irrigated agriculture/short vegetation and evergreen forest classes in the satellite images. Therefore, INEGI series VI vegetation classifications (INEGI, 2017) corresponding to these vegetation types were used to determine the spatial extent of these subclasses (Table I, Fig. 8). Validation of the 2020 vegetation classes was done using 967 reference points randomly placed within the study area. The vegetation classification corresponding to each of these points was compared with vegetation types in higher resolution Google Earth images captured during the dry season from 2017-2020. Errors of commission and omission were calculated in a confusion matrix of these validation points (Table III).

2.4 Estimation of evapotranspiration

Various methods have been developed to estimate ET from specific vegetation types to ET at a regional scale (Fisher et al., 2011). The purpose of estimating ET in this study was not to determine the most accurate values for each vegetation type, but rather to determine the processes that have occurred in the study region which may be influencing ET, and as result, atmospheric water vapour and orographic precipitation in the Sierra Madre. These included changes in temperature, vegetation types and cover, and seasonal changes in leaf cover which is largely influenced by rainfall patterns (Gómez-Mendoza et al., 2008).

Potential ET (PET) is a calculation of the potential amount of water vapour re-entering the atmosphere through ET from the land surface and plants (Xiang et al., 2020). This is based on mainly climatic variables, whereas actual ET is also influenced by vegetation characteristics (Allen et al., 1998). To estimate actual ET in the study area, a method incorporating PET calculations with regional vegetation index values was used (Glenn et al., 2011). This method has been used in other tropical mountain environments (Ramón-Reinozo et al., 2019).

2.4.1 Step 1

We first determined the most appropriate PET calculation method to use. The Penman Monteith (PM) method is often used as the standard to calculate PET but this requires a larger number of environmental data inputs which are not available in most weather stations in Chiapas. Previous analysis comparing the results of PET methods requiring data which are available from all stations in Chiapas with the PM method was done using data from seven *Estaciones Meterológicas Automáticas* (EMAS) weather stations located within or near to the study area (SM Table III; CONAGUA, 2020). These stations collected all the variables required for the comparisons of methods. On average, the Turc method (Turc 1961) produced values closest to the PM value, especially in the mountain areas (SM Table III), therefore this method was chosen to calculate regional PET.

2.4.2 Step 2

PET was calculated with data from 49 weather stations within the study area. Estimations of temperature at three additional locations, based on temperatures or interpolations of temperatures recorded at nearby weather stations at similar elevations in the Sierra Madre (El Triunfo, El Porvenir; SM Table 1) were also included to produce a more accurate interpolation of PET at the higher elevation areas (Sierra Madre 1, 2, and 3; SM Table 1). The average long-term values of Tmin, Tmean, and Tmax were calculated for each station using the value of the least squares regression line at the years 1990, 2005, and 2020. Values were calculated for these years for the same seasons as the temperature trend data: dry-cool representing the wet to dry transition season, dry-hot representing the dry season, and the wet season. PET values calculated for these years and seasons corresponded with the vegetation image layers created (described in the next steps). Raster layers of PET were created using the TIN method in QGIS.

2.4.3 Step 3

The Normalized Difference Vegetation Index (NDVI) was used as the vegetation index to include vegetation characteristics in the ET estimation. Satellite images from the transition, dry, and wet seasons captured within three years of 1990, 2005, and 2020 were used to create the NDVI images (SM Table II).

2.4.4 Step 4

A second vegetation index formula was used to standardize the images. In the NDVI images, the vegetation cover most similar to the reference vegetation used to represent conditions where PET would be equal to actual ET was irrigated agriculture (mainly sugar cane in the Coast region; Aguilar-Rivera et al., 2012), which had an average NDVI value of 0.82. Therefore, this value was used as the NDVI reference value ($NDVI_{ref}$) so that PET would be representative of the estimation of ET in this vegetation type. Denser vegetation types such as evergreen forest would have a higher estimate of ET and seasonal leaf producing vegetation types such as scrub, fields or deciduous forest during the dry season would have a lower estimate. This is representative of the natural conditions in similar mountain regions (Holwerda et al., 2013). $NDVI_{min}$ is the lowest NDVI value in the image. Zero was used for this value.

$$VI = 1 - (NDVI_{ref} - NDVI) / (NDVI_{ref} - NDVI_{min}) \quad \text{Eq. (1)}$$

2.4.5 Step 5

The estimation of daily ET was then done by multiplying the PET layer obtained from the Turc calculation (step 2) and the VI layer (step 4), which replaces the standard crop coefficient in agricultural ET estimations in order to represent natural vegetation types (Glenn et al., 2011).

$$ET = PET \times VI \quad \text{Eq. (2)}$$

INEGI Series VI layers corresponding to the vegetation classes in this study (Table I) were used to separate ET estimations by vegetation type from the raster layers of the regional ET estimations. These raster cuts were used to estimate the mean and standard deviation of ET for each vegetation type (Table IV).

2.5 Local climate and vegetation change relations

O'Brien (1998) determined that local temperature trends were related to a higher degree with forest cover change within a radius of between 0.5 km and 3 km from weather stations in the Lacandon Rainforest in Chiapas, with the relationship less evident as radius sizes increased or decreased from this range. Therefore, in our study, changes in forest cover and NDVI between 1990 and 2020 during the dry season were calculated within a 2 km radius of each station where there was a significant Tmean trend. At these locations, the correlation between forest cover (evergreen, semi-deciduous, and deciduous) and NDVI changes with temperature change was tested using Spearman’s correlation test.

3. Results

3.1 Temperature trends and changes

The average Tmin in the Sierra Madre increased from 1990 to 2016 in all three seasons. In the dry-cool season Tmin increased by 0.2 ± 2.2 ^{o} C, in the dry-hot season by 0.4 ± 1.7 ^{o} C, and in the wet season by 0.5 ± 1.9 ^{o} C. During the same period, the Tmax decreased during the dry-cool season by 1.8 ± 1.2 ^{o} C, the dry-hot season by 1.2 ± 1.3 ^{o} C and the wet season by 1.9 ± 1.3 ^{o} C. The average Tmean also decreased during the dry-cool season by 0.8 ± 1.4 ^{o} C, 0.2 ± 1.3 ^{o} C during the dry-hot season and 1.9 ± 1.3 ^{o} C during the wet season.

In the lower elevation regions, there was a similar pattern with increases in Tmin during the dry-cool (Coast 1.1 ± 1.23 ^{o} C), dry-hot (Coast 1.3 ± 1.1 ^{o} C; Central Depression 0.6 ± 1.6 ^{o} C), and wet seasons (Coast 1.5 ± 1.1 ^{o} C; Central Depression 0.7 ± 1.8 ^{o} C). The exception was the 0.5 ± 1.6 ^{o} C decrease in Tmin during the dry-cool season in the Central Depression. There was also a similar pattern to the Sierra Madre in average Tmax change with decreases in the lower elevation regions during the dry-cool (Central Depression 1.6 ± 1.6 ^{o} C), dry-hot (Coast 0.3 ± 1.1 ^{o} C; Central Depression 0.4 ± 1.9 ^{o} C), and wet seasons (Coast 0.4 ± 1.1 ^{o} C; Central Depression 1.0 ± 1.4 ^{o} C). There was no change in average Tmax during the dry-cool period in the Coast region.

Within Pacific Chiapas, there were 48 significant trends (Mann-Kendall $p<0.05$) determined for Tmean between 1990 and 2016 during the three seasons. Of these, 25 were positive (warmer) trends and 23 were negative (cooler) trends (Fig. 4, SM Table IV). 17 of these significant trends in temperature were from changes of 2.5 ^{o} C or greater. Of these, 5 were cooler trends and 12 were warmer. Of the 10 significant temperature trends shown in the Sierra Madre, only one was a warmer trend, during the dry-hot season.

Where data were available between 1960 and 2016, five significant earlier period (1960-1989) trends contrasted in direction (cooler/warmer or reverse) with later period (1990-2016) trends at the same weather station. All significant 1990-2016 temperature trends (almost all warmer) in the Coast were also significant during the longer 1960-2016 period, whereas significant cooler 1990-2016 trends in the Sierra Madre were not significant during the period since 1960 (Fig. 6, SM Table VI).

3.2 Rainfall trends and changes

In the Sierra Madre, there was little change in monthly rainfall during most of the dry season from January until April. In May, which is typically at the end of the dry season, rainfall increased greatly and this trend continued during the wet months from June until September. At the end of the wet season in October, areas within the El Triunfo and Volcán Tacaná biosphere reserves in the Sierra Madre showed dryer trends and La Sepultura, Frailescana, and the southeast region of El Triunfo, wetter trends. The months of the early dry season in November and December had average rainfall decreases between 1990 and 2016 (Fig. 5). There was a similar, but less extreme pattern of regional averages of monthly rainfall changes in the lower elevation regions, however the largest increases in rainfall occurred at the end of the wet season during the month of October (104 ± 117 mm) in the Coast region (Fig. 5, SM Fig 1).

The average wet season began 7.5 ± 10.6 days earlier between 1990 and 2016 in the Sierra Madre, which corresponds to the wetter trend in rainfall in May. The average end of the wet season was also earlier by 4.9 ± 8.4 days, due to dryer trends in October in some parts of the Sierra Madre. On average, the length of the wet season increased by 2.7 ± 13.6 days, although this varied greatly with the central portion of the Sierra Madre increasing, and the south-east portion near to Volcán Tacaná decreasing in length (Fig. 7). The average wet season also began earlier in the lower elevation regions (Coast 6.2 ± 13.2 days; Central Depression 7.8 ± 15.1 days) but in contrast to the Sierra Madre, ended later (Coast 1.1 ± 9.4 days; Central Depression 4.2 ± 10.5 days).

Twenty-one significant monthly rainfall trends (Mann-Kendall $p<0.05$) were determined within Pacific Chiapas. All were positive (wetter) and occurred during the months from the end of the dry season/beginning of the wet season in May until the end of the wet season in October. There were negative (dryer) trends recorded at some of the weather stations within the study area, however these were non-significant. Many of the significant trends were registered within the Sierra Madre or coastal foothills of the Sierra below 1000 m, and values of changes in monthly rainfall ranged from 110 mm to 650 mm. The greatest increases in monthly rainfall occurred in some the coastal areas during the months of June and September, and in the Sierra Madre each month from June to October (SM Table V). Of these, only one significant rainfall trend was also significant during the 57-year period from 1960-2016 at the Metapa de Dominguez weather station in the Coast region, with a wetter trend for the month of September (Fig. 6, SM Table VI).

3.3 Changes in vegetation types and evapotranspiration

The difficulty in determining boundaries between vegetation types with similar characteristics is shown in the results of the confusion matrix of the vegetation classification validation (Table III). There was an over classification of evergreen forest within the palm plantations and mangrove types due to the similarities of these forests, especially with the 30 m^2 resolution of Landsat images. There was also a higher overlap in classification of deciduous vegetation with gradients between types. The overall accuracy of the 2020 vegetation classification was 82%.

Between 1990 and 2020, the combined area of evergreen and semi-evergreen forest types (cloud forest, rainforest, oak, pine and other coniferous forests, fruit tree, palm plantations and mangroves) increased in area in all three regions. In the Central Depression, these forest types increased by 14%, in the Sierra Madre by 3%, and in the Coast by 22%. However, with the inclusion of deciduous forest as part of the overall forest areas, forest cover decreased from 1990 to 2020 in the

Central Depression. Deciduous forest has characteristics similar to the scrub type and the boundary is not always clear in the satellite images or in the field, as there can be a gradient between deciduous tree cover and shrubby savanna. The area of scrub vegetation and grassland/temporary agriculture can also change throughout the year, as large areas of land which had grown to become scrublands are burned each year to clear land for cultivation. The combined land cover of deciduous forest or scrub decreased by 5% in the Central Depression but increased by 22% in the Sierra Madre and 85% in the Coast (Fig. 8, Table II).

These changes in vegetation types created conditions of larger areas of leaf covered forests in the transition and dry seasons in all regions. Leaf producing forest cover also increased in the Sierra Madre and Coast regions during the wet season, but not in the Central Depression where with the inclusion of deciduous forests which produce leaves in the wet season, overall leaf producing forest area decreased (Fig. 9). These seasonal and long-term changes can also be seen in the average values of the NDVI (SM Table VIII), which increased in all regions for all three seasons between the 1990 and 2020 images. Increases in the NDVI between the 1990 and 2020 images in the wet season in the Central Depression could be due to denser growth of the scrub vegetation type or a lower NDVI value at the end of the wet season (November) in the 1990 image compared to the earlier date of the image captured in the 2020 wet season (August). Most of the 1990 to 2020 (30-year) comparisons were done between similar times of the year, but there were no Landsat images during the 1987-1993 wet season without large amounts of cloud cover, so the use of an image captured in November was the best option available.

These vegetation index (live green vegetation density) increases, which theoretically would create conditions of greater ET, were offset by decreases in PET between 1990 and 2016, during all three seasons. These decreases were due to the overall regional temperature changes, which were on average warming Tmin and cooling Tmax. Overall decreases in PET were outweighed by the increases in vegetation index and estimated ET increased between 1990 and 2020 from 2.70 mm/day to 2.83 mm/day in the transition season, 2.83 mm/day to 3.16 mm/day in the dry season, and without change in the wet season. However, there was variation in the direction of changes between these years with an increase in estimated ET between 1990 and 2005 and a decrease between 2005 and 2020, during the transition season. ET decreased slightly between 1990 and 2005 and then increased between 2005 and 2020 during the dry and wet seasons (Fig. 10).

During the 2020 dry season, the highest amounts of ET were estimated for the coastal low elevation, evergreen vegetation types: mangrove, palm plantation, and coastal wetland (Table IV). These were followed by the mountain evergreen vegetation types: shade coffee, high elevation evergreen forest, low elevation evergreen forest, and lower elevation irrigated agriculture. Lower ET were estimated for deciduous or dry vegetation types: deciduous forest, scrub, and non-irrigated land. During the wet season, when all the vegetation types produce green leaves, the denser, low elevation vegetation, including deciduous forest had the highest estimation of ET. ET decreased with vegetation types at higher, cooler elevations on the Sierra Madre. During the transition season, the highest amounts of ET were in the lower elevation evergreen vegetation types, with ET decreasing in the higher elevation evergreen types and the lowest amounts in the deciduous vegetation types as leaves dry and fall.

During the dry season, estimates of ET increased from 1990 to 2020 in all vegetation types, except the high elevation evergreen forest were there was no change (Table IV). During the wet season, ET only increased in the lower elevation vegetation types between 1990 and 2020 and decreased in the mid to higher elevation forest and coffee plantation vegetation. There was little change in the scrub type. Lower elevation vegetation types also had increases in ET during the transition season, except for the coastal wetland which had a decrease. ET also increased in the mid elevation semi-evergreen forest during this season. The evergreen forest types and coffee plantations on the Sierra Madre had decreases in ET.

3.4 Relation between local climate trends and vegetation changes

There was no clear correlation between vegetation changes within a 2 km radius of weather stations where there was a significant trend in Tmean, and changes in Tmean at these locations. This was the case for both changes in NDVI (p=0.88), and percent change in forest cover (p=0.85). Some areas which had experienced reductions in forest cover between 1990 and 2020 had positive trends in Tmean, whereas others had negative trends. Likewise, areas that experienced gains in forest cover had either positive or negative Tmean trends.

4. Discussion

4.1 Comparisons of 1960-2016, 1990-2016 trends and large-scale climatic influences

The generally wetter wet seasons and dryer dry seasons during the 1990-2016 period in all three regions were consistent with global trends in precipitation (Murray-Tortarolo et al., 2017) during a similar time period (1980-2005). Murray-Tortarolo et al. (2017), discussed that these trends may have been the result of global oceanic (La Niña years) and atmospheric (1991 Mt. Pinatubo eruption) conditions during the late 1980's and early 1990's, which lowered global precipitation during these years, and the beginning of global warming influences. However, the relation between rainfall and La Niña are variable within Mexico and are generally associated with higher rainfall in Southern Mexico (Bravo-Cabrera et al., 2017). The lack of significant trends in rainfall in Pacific Chiapas during a longer time period (1960-2016) at most weather stations where there was a wetter trend during the 1990-2016 period, was also consistent with global trends (Murray-Tortarolo et al., 2017), except for an area of the Coast (Metapa de Dominguez during September; Fig. 5, SM table VI) where there was an extended 57-year significant wetter trend.

Significant cooler trends between 1990-2016 in the Sierra Madre were not significant since 1960, which contrasted with the longer continuation of significant warmer trends in the Coast. Increasing trends in rainfall since 1990 in the mountain region may be related to the cooler trends during 1990-2016 (mostly due to decreases in Tmax; Fig. 4) at higher elevations because of greater cloud cover.

Regional climatic trends between 1990 and 2016 in Pacific Chiapas were consistent with those attributed to the effects of long-term trends in the Pacific Decadal Oscillation (PDO) in southern Mexico (Méndez-González et al., 2010). During this period, the PDO index showed a negative trend from a positive phase in the 1990's to a negative phase in the 2000's (NOAA, 2020b). Méndez-González et al. (2010) determined that from 1950-2007, negative periods of the PDO have been associated with higher summer precipitation, cooler summer Tmax, and warmer Tmin, in southern Mexico. These trends were determined on average for the study region, although not consistently for all weather stations, especially in some parts of the Coast, which had increases in both Tmin and Tmax (Fig. 4).

Summer rainfall in Chiapas is also strongly influenced by the ITCZ bringing moisture from the Caribbean Sea and Gulf of Mexico. SST have increased both in the Gulf of Mexico and the Caribbean since 1975 (Lluch-Cota et al., 2013), and higher amounts of evaporation from a warmer surface may increase atmospheric moisture and intensify downwind rainfall (Brito-Castillo, 2012). Increases in rainfall often indicate cloudier conditions and this can affect regional temperatures (Englehart and Douglas, 2005), effects consistent with the determined regional trends. Increased cloud cover blocks incoming day time solar radiation, lowering Tmax, whereas nighttime Tmin are increased by the insulation of cloud cover, which reemits longwave radiation back to the ground. The predicted climate effects of increases in global atmospheric CO_2 from 1990 amounts described by Liverman and O'Brien (1991) for the southern Pacific region of Mexico were also consistent with those determined by this study for rainfall patterns, although the predicted temperature increases were only determined on average for Tmin.

4.2 Relations between land use change, vegetation and climate trends

Between 1970 and 2000, Chiapas experienced large amounts of deforestation (Richter, 2000; Solórzano et al., 2003). However, reviews published in the years after 2000 began to discuss a possible change in the rate of deforestation and beginning of reforestation in parts of Mesoamerica (Bray, 2009). Evidence supporting this prediction may be shown by Vaca et al. (2012) who reported a decreased annual rate of deforestation between the periods of 1990-2000 and 2000-2006 in the dry tropical forests of the Central Depression of Chiapas. Bonilla-Moheno and Aide (2020) also reported an increase in forest cover in the lower elevation, inland portion of the Sierra Madre between 2001-2014, which was consistent with what was determined in this study.

The abandonment of agricultural areas during increased urban migration, and the large scale of land which had already been deforested by the year 1990 may have contributed to increased forest cover in the areas adjacent to the Sierra Madre between 1990 and 2020 (Bonilla-Moheno and Aide, 2020). Trends of increasing rainfall in these regions may also have been influential for regeneration of forests in abandoned agricultural areas, even when there were large variations in rainfall between years (Martínez-Ramos et al., 2018). The steep and less accessible Sierra Madre region was by far the most forested of the study area, with very little overall change in forest cover. The establishment of Biosphere Reserves beginning in 1990, and programs such as Payment for Hydrological Environmental Services within communities of the Sierra Madre influenced the slower changes in this region (Cano-Díaz et al., 2015).

Large differences in species composition can exist between vegetation types which are difficult to distinguish remotely, such as regenerating deciduous forests and native scrub ecosystems (Gordillo-Ruiz et al., 2020). Species composition, diversity and succession stage can influence differences in vegetation responses to climate trends and ET (Ballinas et al., 2015; Sakschewski et al., 2016). Additionally, topography, vegetation cover, and soil characteristics of landscapes can influence water availability from rainfall (Ponette-González et al., 2010; Schwartz et al., 2019); and vegetation can have physiological responses to changes in climate allowing them to regulate ET (Massmann et al., 2019). These physiographic and physiological characteristics indicate a limitation of the modelling we used to estimate ET. We hope our regional focus inspires further field-based studies of ET in the specific vegetation types we have included. However, the use of local climatic data and remote sensing, which showed increases in dense vegetation cover and regional estimations of ET between 1990 and 2020, were useful to understand the contribution of vegetation changes to the climate of Pacific Chiapas, in particular the coastal mountains.

Regional increases in forest vegetation and ET may have contributed to a positive climatic feedback, which combined with the influences of increasing SST in the east coast of Mexico, a negative phase of the PDO in the west coast, and increasing atmospheric CO_2, produced larger positive trends in rainfall during the late dry and wet seasons. Estimates of ET mainly decreased in the mountain evergreen forests between 1990 and 2020 (Table IV) due to decreasing trends in temperature (Fig. 4). However, there were overall increases in estimated regional ET, due to increases in the density of leaf producing vegetation cover and some regional temperature increases, especially in the lower elevation regions (Fig. 10, SM Table VIII). There is also a strong relationship between the onset of the wet season and the production of leaves in deciduous and semi-deciduous vegetation in Mexico (Gómez-Mendoza et al., 2008). The earlier trend in the start of the wet season in this region may indicate that leaf production is beginning earlier in the year and that, along with increases of available soil moisture, could result in earlier increases in ET, contributing to higher atmospheric moisture and higher orographic rainfall in the Sierra Madre.

Increases in semi-deciduous and evergreen forest cover between 1990 and 2020 may cause greater regional latent heat flux, decreases in sensible heat flux (Ray et al., 2006a; Ray et al., 2006b), and increases in surface roughness (Spracklen et al., 2018). This may affect heights of orographic cloud cover, which potentially could decrease with these land cover change conditions (Lawton et al., 2001; Fairman et al., 2011), and affect the altitudinal distribution of rainfall (Barradas et al., 2010). The constant burning of regenerating deciduous forest and savannahs for seasonal agriculture in the Central Depression create conditions of higher surface albedo, which can negatively affect rainfall (Fuller and Ottke, 2002). This may be another reason for the lower regional increases in rainfall in the Central Depression in comparison with the much greater forested Sierra Madre region.

At various locations, significant climate trends differed from the overall average regional changes (Fig. 4, Fig. 5, SM Table IV, SM Table V). There were no clear relations between local significant temperature or rainfall changes and vegetation changes (forest cover or NDVI). This suggests that the regional climate changes determined were influenced to a greater extent by long term atmospheric and oceanic processes and regional vegetation changes. Local differences in temperature and rainfall patterns may be due to topography, air flow patterns, and the orographic nature of precipitation in this mountainous region, as in other parts of Mesoamerica (Barradas et al., 2010; Maldonado et al., 2018).

Many of the ocean influence patterns are cyclical at a time scale greater than the study period of 27 years (Fuentes-Franco et al., 2015). Therefore, the climate trends and patterns determined in this study may change as trends change in the large-scale climatic influences which affect Chiapas (Aguilar et al., 2005). However, if increasing vegetation cover trends continue in this region, they may moderate future climate cycles in the Sierra Madre (Lawton et al., 2001; Bonan, 2008).

5. Conclusion

Regional 1990-2016 climate trends within Pacific Chiapas included increases in Tmin, decreases in Tmax, an earlier shift in the wet season and greater amounts of rainfall within this season. All significant temperature trends continued from 1960-

2016 in the Coast region but less so in the Central Depression and did not in the Sierra Madre. Only one significant rainfall (wetter) trend continued during this 57-year period, in an area of the Coast. The more recent (1990-2016) trends occurred during a period of change in ocean and atmospheric climatic influences on the region, including a negative trend in the PDO index, warming SST in the Gulf of Mexico and Caribbean, and rising amounts of atmospheric CO_2. During the same time period, regional extents of evergreen and semi-evergreen forest types, NDVI values, and estimates of ET increased. These changes may have enhanced the climatic patterns influenced by large-scale processes.

Acknowledgements

We thank the two anonymous reviewers for their helpful comments to improve the article. The first author received a doctoral scholarship from CONACyT (No. 884660).

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Tables and Figures

Table I. Elevation range of vegetation types within the study area according to the Instituto Nacional de Estadística y Geografía (INEGI, 2017) classification, which were included in the classification of the general vegetation type.

General vegetation type	**INEGI classification**	**Elevation range (m a.s.l.)**
Evergreen forest (higher elevation)	Fir (*Abies* sp.) forest	2000-2900
	Cloud forest	700-4000
	Pine forest	500-2500
Evergreen forest (lower elevation)	Secondary tall rainforest	200-1400
	Riparian forest	600-700
	Riparian rainforest	0-700
Shade coffee plantation	Permanent agriculture	300-2000
Semi-deciduous forest	Pine-oak forest	800-2500
	Oak-pine forest	400-1900
	Semi-deciduous forest	400-1500
	Oak forest	600-1200
	Fruit tree plantations	10-25
	Palm forest	0-5
Deciduous forest	Deciduous tropical forest	300-1700
	Low spiny forest	0-10
Mangrove	Mangrove	Sea level
Palm plantations	Permanent agriculture	10-50
Scrub	High mountain vegetation	3500-4000
	Temporary agriculture	400-2500
	Herbaceous vegetation	550-850
	Savannah	30-800
	Cleared vegetation	50-250
Short vegetation	Irrigated agriculture	5-700
	Coastal dune vegetation	Sea level
	Coastal wetland (Tular)	Sea level
	Coastal wetland (Popal)	Sea level
Grassland/seasonal agriculture	Grassland	0-1000
	Temporary agriculture	0-900

Table II. Areas (ha) of vegetation types in 1990 and 2020 within the three physiographic regions of the study area (Central Depression, Sierra Madre, Coast), and these three regions together (Pacific Chiapas). The percent of regional area of each land cover are shown within parenthesis next to the area values.

Vegetation type	**Year**	**Area (ha) and percent of each vegetation type**			
		Central Depression	**Sierra Madre**	**Coast**	**Pacific Chiapas**
Evergreen forest	1990	43663 (3)	328565 (60)	152917 (17)	525145 (19)
	2020	70866 (6)	351099 (64)	172090 (19)	594055 (22)
Semi-deciduous forest	1990	238366 (19)	128683 (24)	144230 (16)	511279 (19)
	2020	251561 (20)	121921 (22)	187219 (21)	560701 (21)
Mangrove	1990	0	0	28549 (3)	28549 (1)
	2020	0	0	36958 (4)	36958 (1)
Palm plantations	1990	0	0	0	0
	2020	0	0	7152 (1)	7152 (<1)
Deciduous forest	1990	331660 (26)	29575 (5)	15932 (2)	377167 (14)
	2020	258537 (20)	15275 (3)	21178 (2)	294990 (11)
Scrub	1990	413594 (32)	13193 (2)	73593 (8)	500380 (18)
	2020	453043 (35)	36996 (7)	144389 (16)	634428 (23)
Agriculture/short vegetation/wetland	1990	31898 (2)	23136 (4)	214166 (24)	269200 (10)
	2020	13837 (1)	6155 (1)	116486 (13)	136478 (5)
Grassland/seasonal agriculture	1990	168002 (13)	15914 (3)	222593 (25)	406509 (15)
	2020	185263 (14)	10137 (2)	149174 (17)	344574 (13)
No vegetation	1990	5062 (<1)	897 (<1)	6458 (1)	12417 (<1)
	2020	5828 (<1)	928 (<1)	16321 (2)	23077 (1)
Water	1990	50753 (4)	0	27839 (3)	78592 (3)
	2020	43723 (3)	0	30129 (3)	73852 (3)

Table III. Confusion matrix of 967 points comparing the vegetation types classified from the 2020 Landsat images (Classification) with the validation in Google Earth (Reference). Vegetation types are evergreen forest (E), semi-deciduous forest (SD), deciduous forest (D), scrub, irrigated agriculture/short vegetation (SV), grassland or seasonal agriculture (Grass), no vegetation (No-V), mangrove (Man), and palm plantation (Palm).

	Reference (Google Earth)										
Classification	E	SD	D	Scrub	SV	Soil	No-V	Man	Palm	Total	Error of Commission (%)
E	159	5	0	5	4	0	0	0	17	190	16.3
SD	11	120	0	11	8	1	0	7	8	166	27.7
D	0	11	61	12	0	2	0	0	0	86	29.1
Scrub	0	8	3	170	1	24	2	1	1	210	19.1
SV	2	2	0	3	93	1	0	3	2	106	12.3
Grass	0	1	0	8	1	126	1	0	0	137	8.0
No-V	0	0	0	0	2	0	9	3	0	14	35.7
Man	0	0	0	0	0	0	0	40	0	40	0
Palm	0	0	0	0	0	0	0	0	18	18	0
Total	172	147	64	209	109	154	12	54	46	967	
Error of Omission (%)	7.6	18.4	4.7	18.7	14.7	18.2	25.0	25.9	60.9		

Table IV. Estimations and standard deviations of evapotranspiration (ET) (mm/day) from the land cover types: high elevation (HE) evergreen, low elevation (LE) evergreen, semi-evergreen forest, shade coffee plantation, mangrove, deciduous forest, scrub, coastal wetland, irrigated agriculture, grassland or seasonal agriculture, and oil palm plantations, in 1990 and 2020 during the transition from wet to dry (Trans.), dry, and wet seasons.

Land cover	**1990 Trans.**	**1990 Dry**	**1990 Wet**	**2020 Trans.**	**2020 Dry**	**2020 Wet**
HE evergreen	3.22±0.52	3.86±0.87	3.97±0.92	3.04±0.54	3.87±0.77	3.54±1.05
LE evergreen	3.24±0.55	3.69±0.92	4.10±0.75	3.12±0.51	3.84±0.84	3.89±0.88
Semi-evergreen	2.88±0.59	3.02±0.77	4.05±0.86	3.02±0.55	3.39±0.85	4.05±0.88
Coffee	3.52±0.47	4.10±0.72	4.01±0.62	3.48±0.43	4.26±0.58	3.95±0.94
Mangrove	3.67±0.74	3.93±0.94	4.05±1.01	3.75±0.66	4.50±0.93	4.12±0.75
Deciduous forest	2.36±0.60	2.26±0.56	4.02±0.82	2.84±0.59	2.95±0.76	4.33±0.80
Scrub	2.53±0.68	2.63±0.86	3.93±0.75	2.65±0.62	2.91±0.86	3.99±0.84
Coastal wetland	3.48±0.51	3.43±1.06	3.93±0.66	3.27±0.58	4.36±0.77	4.29±0.78
Irrigated agri.	3.12±0.84	2.94±1.03	4.03±0.57	3.12±0.74	3.45±1.10	3.98±0.89
Grassland	2.28±0.61	1.99±0.51	3.71±0.84	2.28±0.61	2.39±0.72	4.01±0.78
Palm plantation				3.76±0.60	4.38±0.92	4.76±0.68

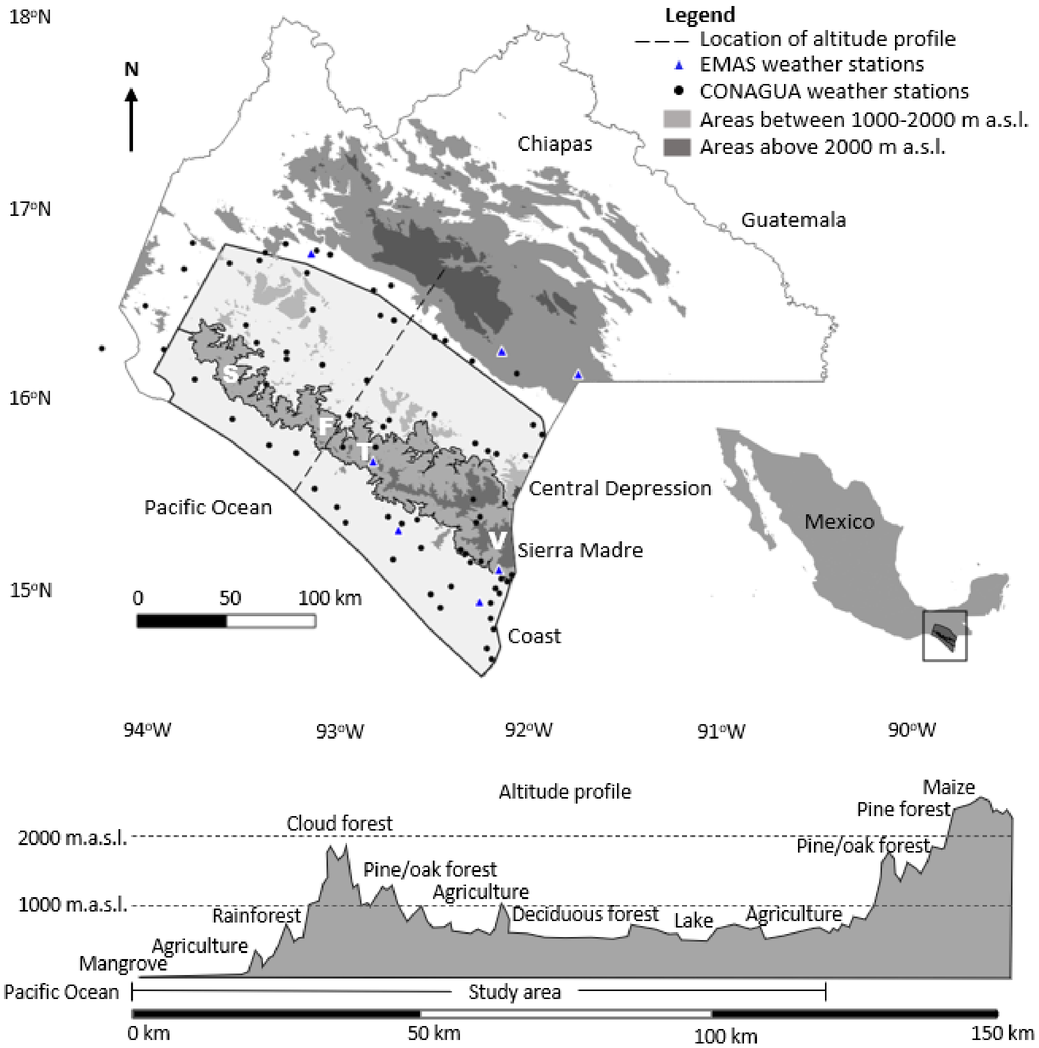

Figure 1. Study area of the Central Depression, Sierra Madre, and Coast regions of Chiapas, Mexico, locations of the weather stations, and an elevation profile from the Pacific Ocean to the Central Highlands of Chiapas. The letters S, F, T and V indicate locations of the Biosphere Reserves: La Sepultura (S), Frailescana (F), El Triunfo (T), and Volcán Tacaná (V).

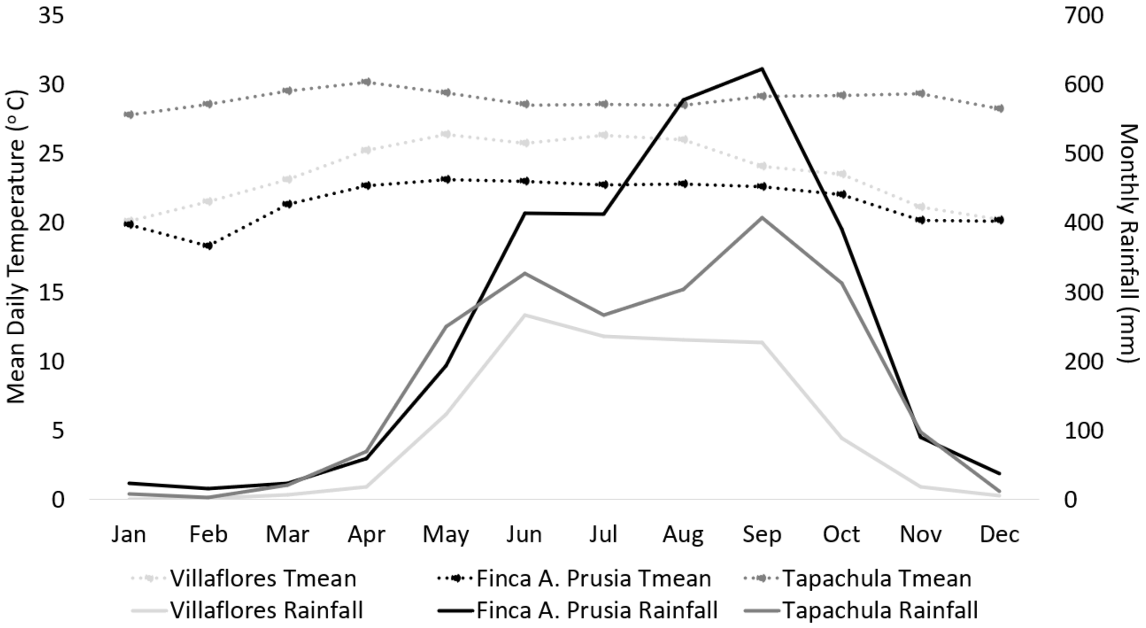

Figure 2. Monthly averages of mean daily temperature (Tmean) and rainfall during the 1990-2016 period in the Central Depression (Villaflores weather station), Sierra Madre (Finca A. Prusia), and Coast (Tapachula) regions.

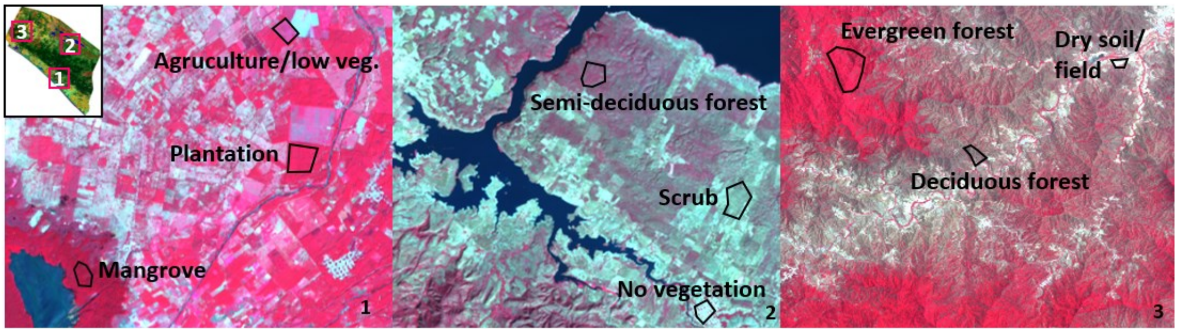

Figure 3: Examples of the vegetation types used for classification in the combination of the green, red, and infrared bands of the satellite images in the Coast (1), Central Depression (2), and Sierra Madre (3) regions of Chiapas, Mexico.

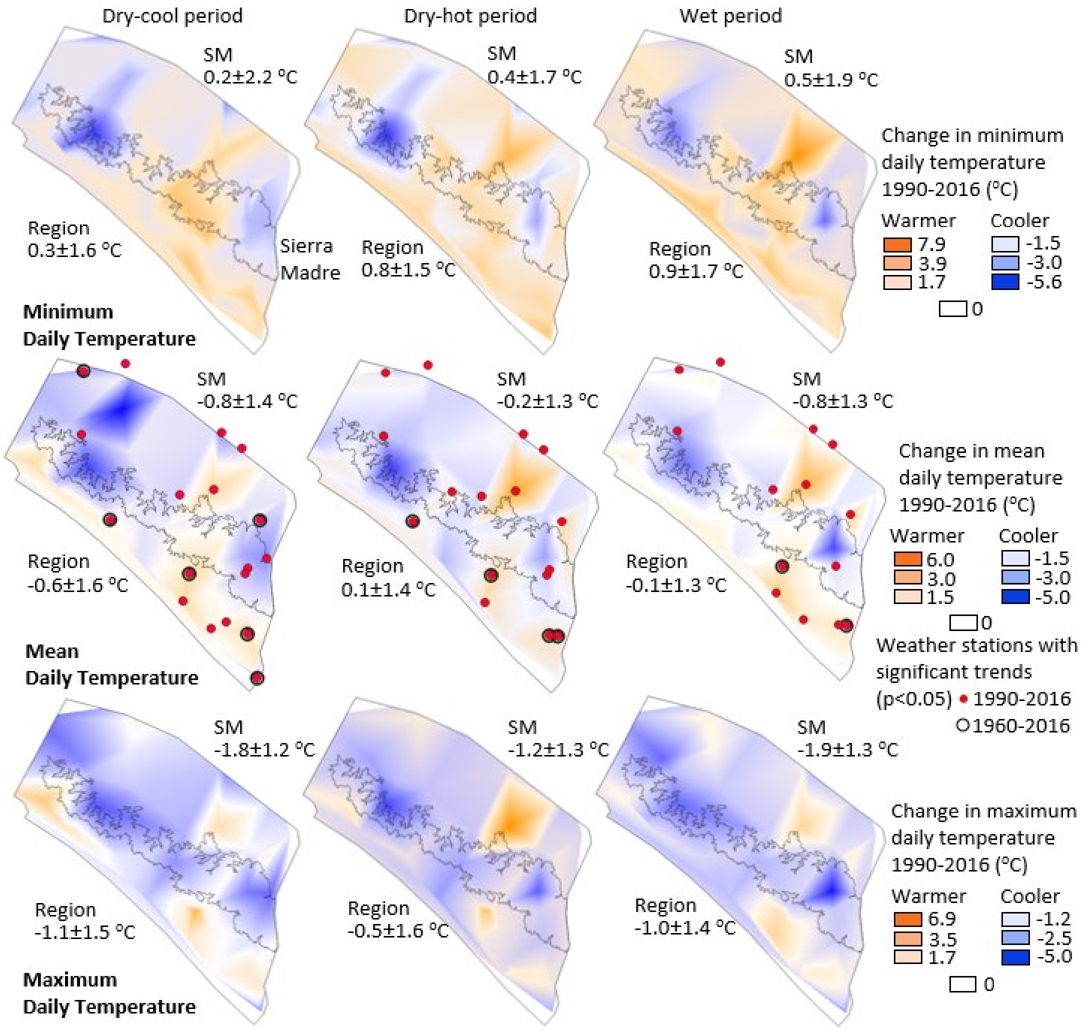

Figure 4. Average daily temperature change between 1990 and 2016 in the Central Depression, Sierra Madre, and Coast regions of Chiapas, Mexico. Cooler temperature changes are shown in blue and warmer changes in orange. Red points indicate locations of weather stations with significant trends in average daily temperature. The mean and standard deviation of temperature changes within the study area are written below *Region* on the map. The mean and standard deviation within the Sierra Madre (SM) region are written below *SM*.

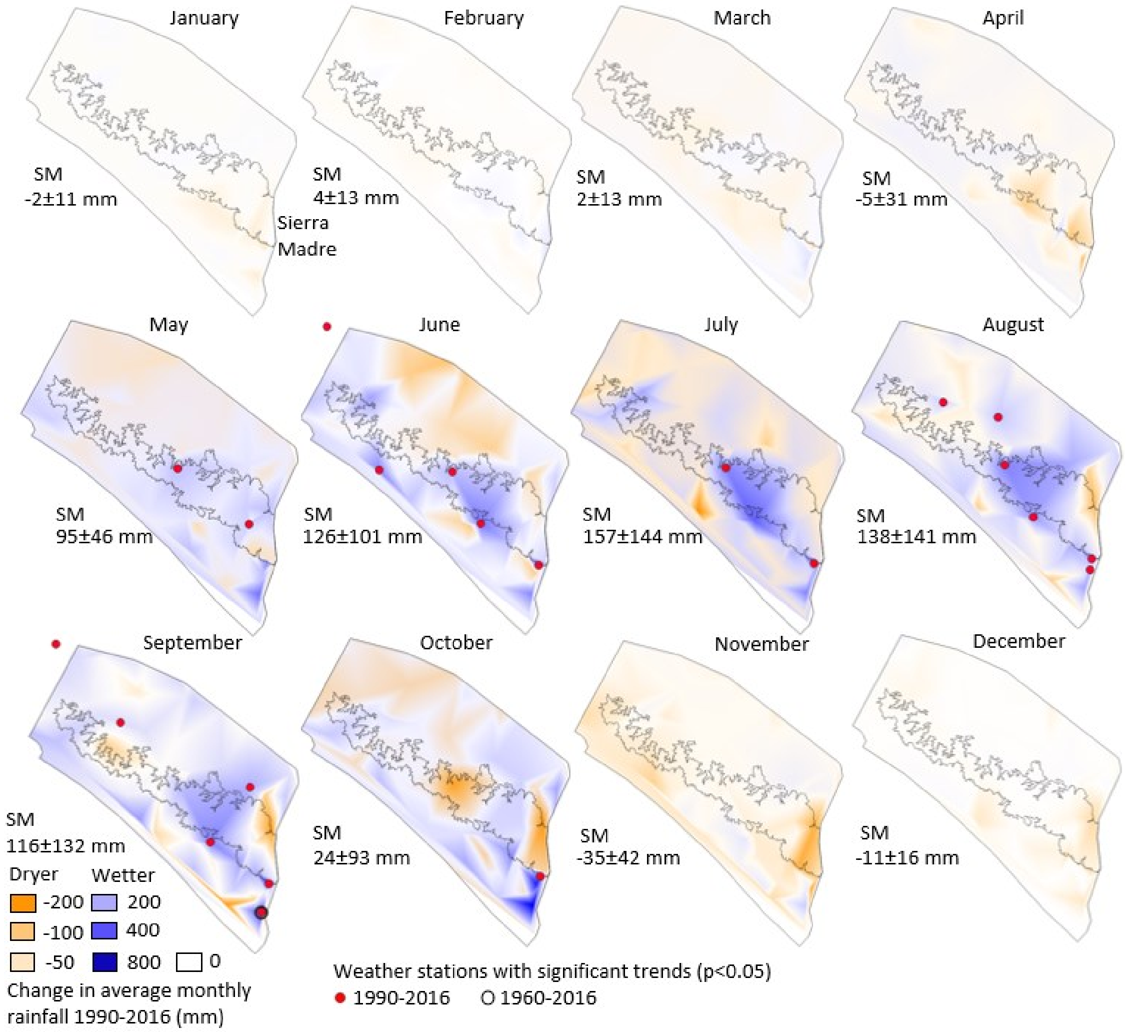

Figure 5. Changes in monthly rainfall between 1990 and 2016 in the Central Depression, Sierra Madre, and Coast regions of Chiapas, Mexico. Wetter changes are shown in blue and dryer changes in orange. Red points indicate locations of weather stations with significant trends in monthly rainfall. The mean and standard deviation of monthly rainfall changes within the Sierra Madre (SM) region are written below *SM* on the map.

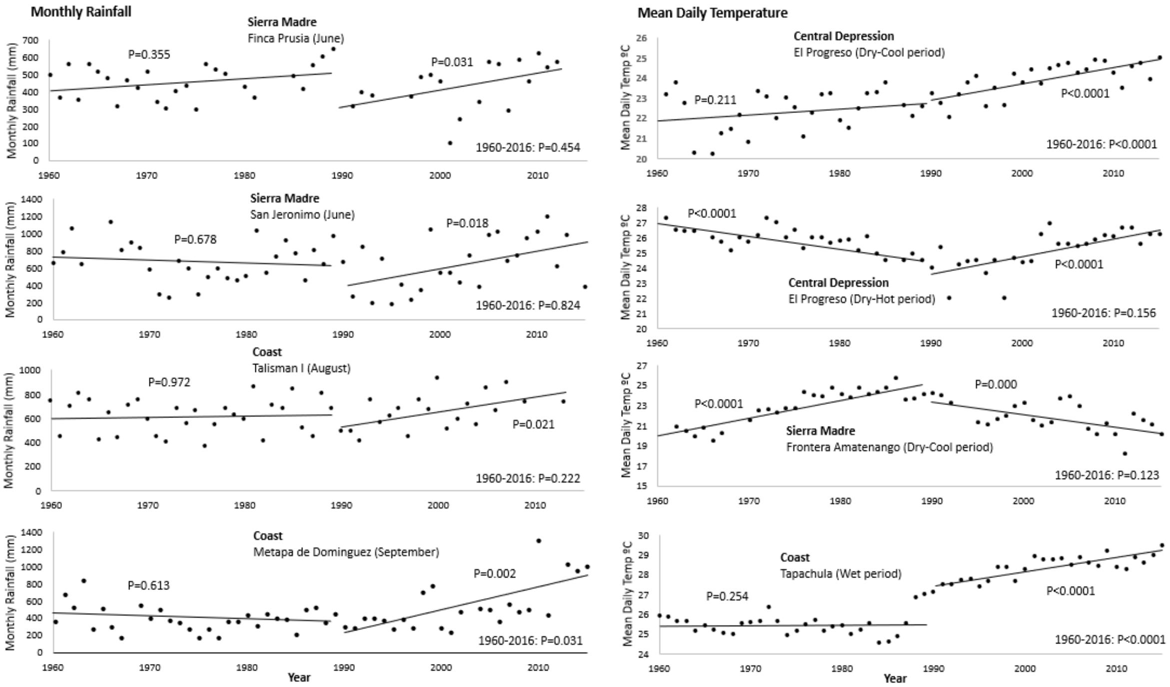

Figure 6. Trends in monthly rainfall and mean daily temperature during the periods 1960-1989 and 1990-2016 for select weather stations in the Central Depression, Sierra Madre, and Coast regions of Chiapas, Mexico.

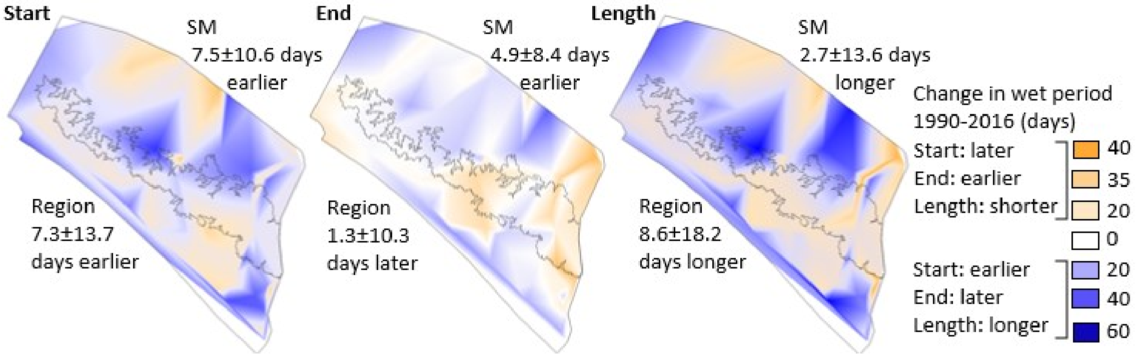

Figure 7. Changes in the number of days between 1990 and 2016 in the start, end and length of the wet season. The mean and standard deviation of changes in days of the start, end, and length of the wet season within the entire study area (Pacific Chiapas) are written below *Region* on the map. The mean and standard deviation within the Sierra Madre (SM) region are written below *SM*.

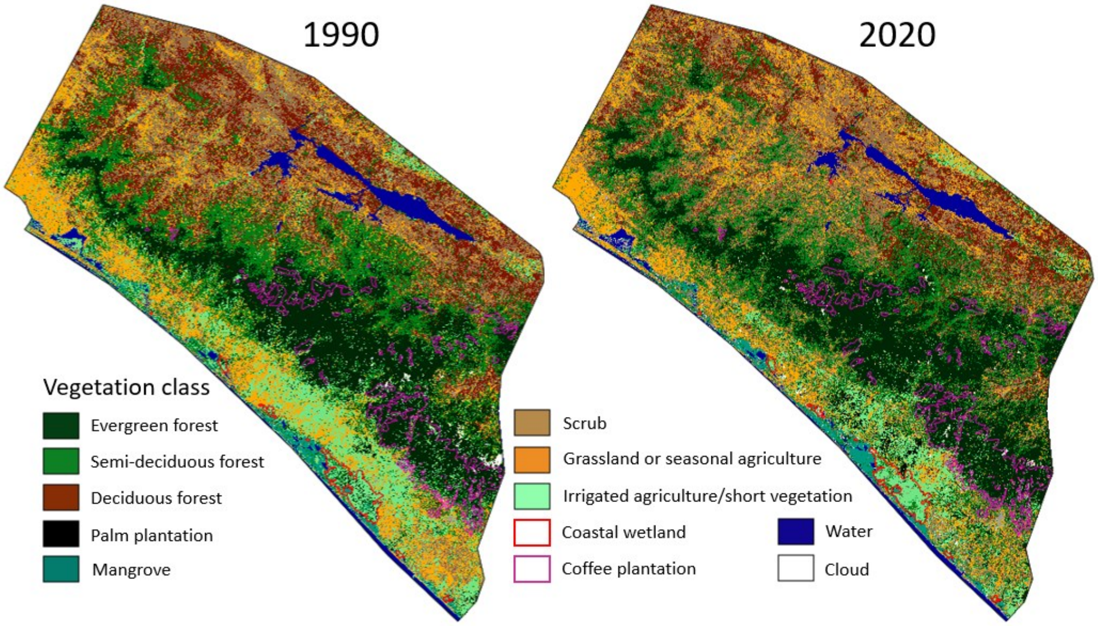

Figure 8. Land cover in 1990 and 2020 in the Pacific regions of Chiapas, Mexico.

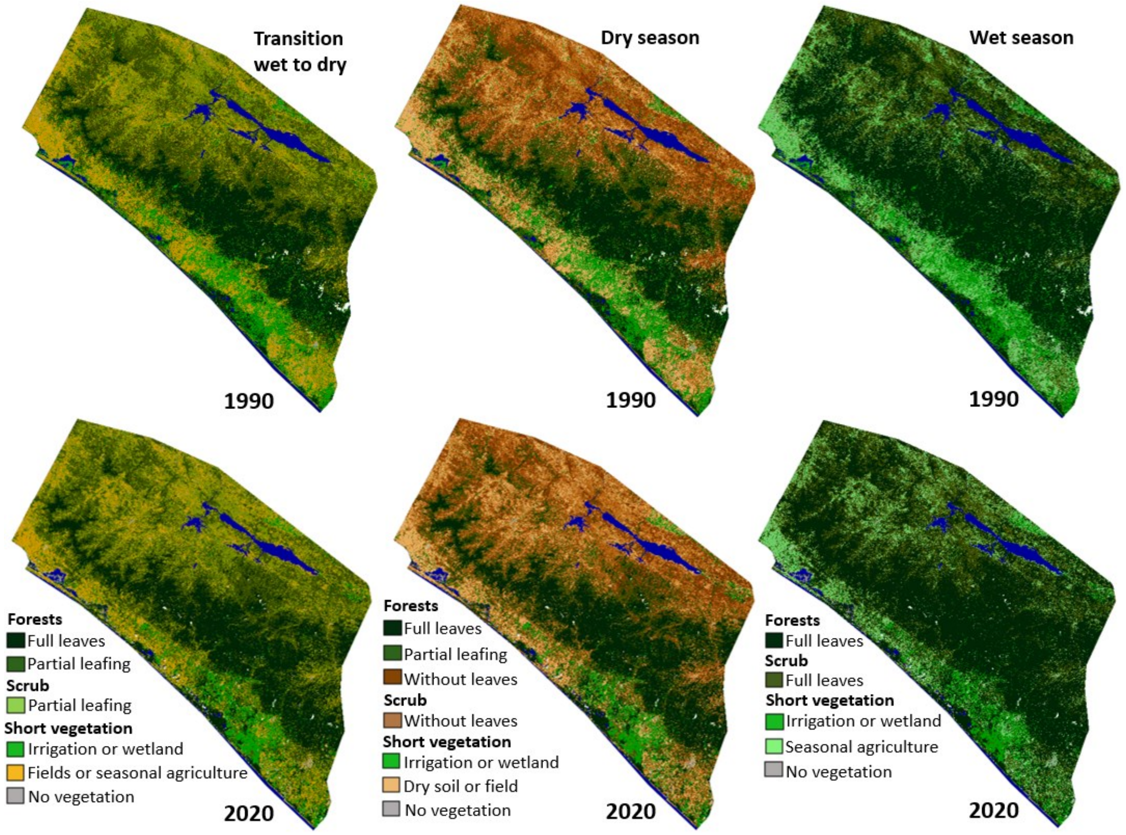

Figure 9. Seasonal vegetation characteristics of the transition from wet to dry, dry, and wet seasons in 1990 and 2020.

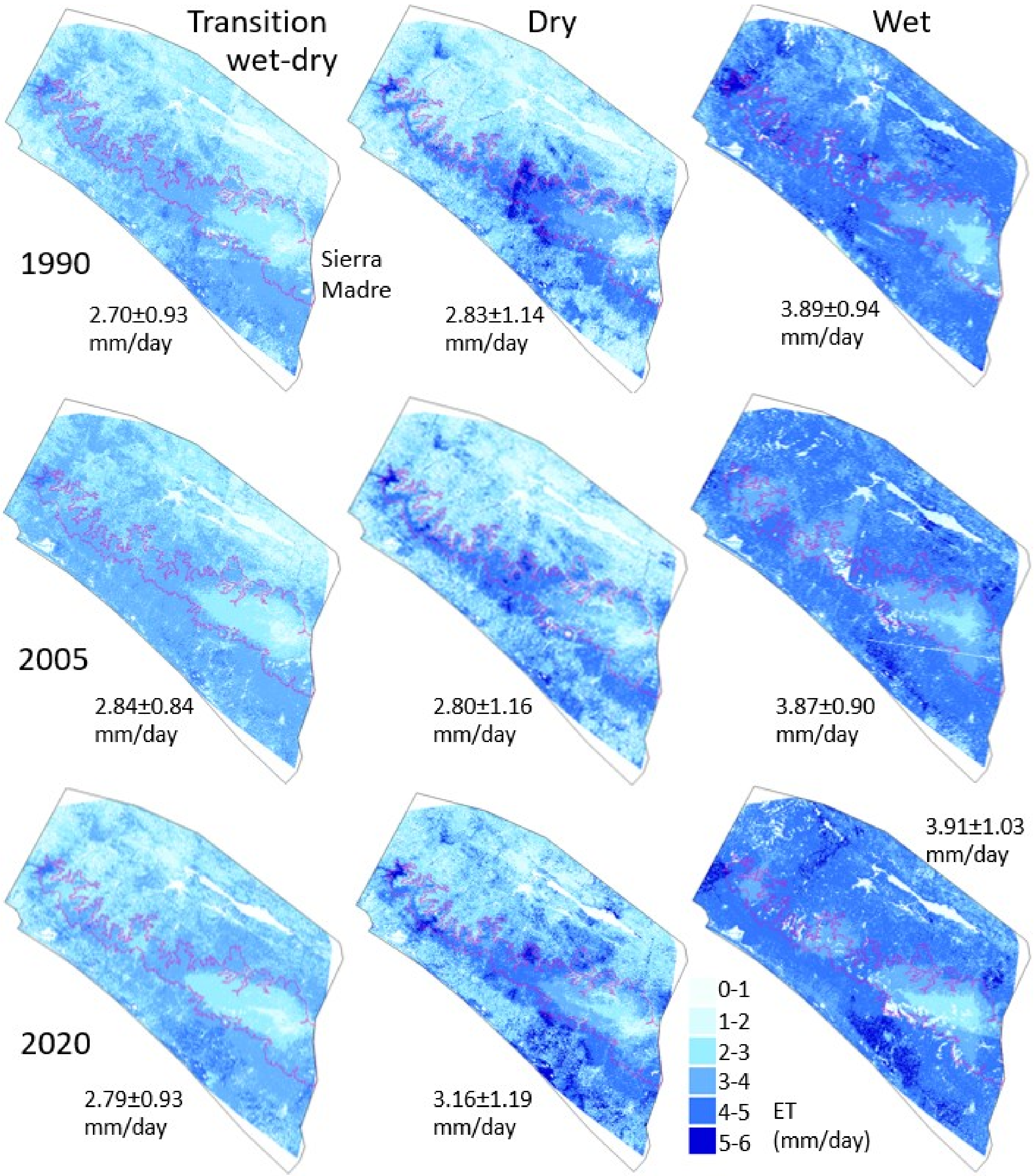

Figure 10. Estimates of evapotranspiration in the transition from wet to dry, dry, and wet seasons of 1990, 2005, and 2020 in the Pacific regions of Chiapas, Mexico. The mean and standard deviation of evapotranspiration within the study area is written next to each image.

CAPÍTULO 3

Frutos de *Citharexylum mocinnii*. Foto de Allen Wootton.

Climate trends, a hurricane, and phenological patterns in El Triunfo cloud forest, Mexico*

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*Manuscrito sometido al Biotropica (Manuscript ID: BITR-21-425)
https://onlinelibrary.wiley.com/journal/17447429

Abstract

Rainfall and temperature conditions have changed within the cloud forests of southern Mexico since 1990, but their effects on tree community phenology are not well understood. The aim of our study was to determine the relationship between seasonal patterns of flowering and fruiting, and the annual and ~30-year changes in temperature and rainfall in El Triunfo Biosphere Reserve, Mexico. Flower, unripe and ripe fruit intensity, fruit number and biomass were recorded for 162 trees of 21 species producing the quetzal's feeding resources during 17 months in 2019-2021. Circular statistics and correlations were used to test relationships between the phenophases and temperature, rainfall, daylength, and solar radiation. Flowering and unripe fruit intensity were negatively correlated with temperature and daylength. Additionally, flowering was negatively correlated with rainfall and unripe fruiting with solar radiation. Ripe fruit number was positively correlated with solar radiation, with overall fruiting peaks before the wet season. We compared recent fruiting seasonality with phenological data collected in 1991-1993. The mean date of community fruit presence in 2019-20 was earlier (March 12) than in 1992 (March 29) and 1993 (May 4). However, after Hurricane Eta in November 2020, fruit presence patterns occurred later in the year by two weeks, and fruit number decreased. Our results suggest that ~30-year trends of increasing minimum daily temperature and an earlier and wetter wet season influenced the timing of community fruiting phenology, whereas an extreme weather event affected the numbers of fruits produced. This could impact the availability of feeding resources for frugivores.

Key words

climate change, flowering, fruiting, frugivores, quetzal, Sierra Madre

1. INTRODUCTION

Yearly and long-term changes in temperature and rainfall affect flowering and fruiting patterns in tropical forests (Chapman et al., 2005; Barnes, 2015; Du et al., 2020; Corredor-Londoño, Beltrán, Torres-González, & Sardi-Saavedra, 2020). However, long term or comparative phenological studies are rare in higher elevation tropical cloud forests, especially in the Neotropics (Mendoza, Peres, & Morellato, 2017). Cloud forests provide important refuge and reproductive habitats for flora and fauna (Rojas-Soto, Sosa, & Ornelas, 2012), and contain a high diversity of endemic species (González-Espinosa, Meave, Lorea-Hernández, Ibarra-Manríquez, & Newton, 2011). The timing of fruit presence could affect the reproduction and migration of animal species in these forests (Bustamante, Barrios, & Juárez, 2010).

In the ecologically and climatically complex systems of wet tropical forests, factors which influence the phenology of tree communities, species or individuals of a species can be both biotic and abiotic. Biotic factors include the timing of interactions between flower production and the arrival of pollinators (Xu & Servedio, 2021), niche partitioning between fruit production characteristics and frugivore dispersers (Todeschini, Toledo, Rosalino, & Hilario, 2020), changes in the allocation of resources between growth and reproduction (Wheelwright, 1986), and the time between flower pollination and fruit production (Bendix et al., 2006). Biotic factors often influence the characteristics of phenological patterns (e.g., numbers of fruits produced, length of fruiting period; Oshima, Tokumoto, & Nakagawa, 2015; Brito et al., 2017) whereas abiotic factors influence the timing of these patterns (Van Schaik, Terborgh, & Wright, 1993; Mendoza et al., 2017).

Abiotic factors include both environmental conditions where within year changes are consistent between years (e.g., solar radiation and daylength; Numata, Yasuda, Okuda, Kachi, & Noor, 2003), or conditions with variability from year to year or long-term trends (e.g., temperature, rainfall, and relative humidity; Bendix et al., 2006; Dunham, Razafindratsima, Rakotonirina, & Wright, 2018). Pau et al.

(2011) discussed the possibility that species with similar phenological patterns from year to year are influenced by factors which change little between years. Species with changes in the timing of phenological patterns between years may be more influenced by factors with yearly variation such as temperature and rainfall (Pau, Cordell, Ostertag, Inman, & Sack, 2020).

The causes of changing phenological patterns within a tropical tree community may be difficult to determine, as species with different life histories can have varying phenological reactions to the same climatic factors (Boyle & Bronstein, 2012). The diversity of species and phenological patterns in the cloud forests of southern Mexico (Solórzano, Ávila, Castillo, Meave, & Ibarra-Manríquez, 2010) indicate that climatic factors may be having different influences on individual species within the forest communities, in areas such as the El Triunfo Biosphere Reserve.

El Triunfo is located parallel to the Pacific coast of the southern Mexican state of Chiapas, in the Sierra Madre de Chiapas. The reserve was established in 1990 with the goal to conserve endemic species and biodiversity of the region, especially within the higher elevation cloud forests. These forests are important reproductive habitats for animal species such as spider monkey (*Ateles geoffroyi*), tapir (*Tapirus bairdii*), horned guan (*Oreophasis derbianus*), emerald toucanet (*Aulacorynchus prasinus*), and quetzal (*Pharomachrus mocinno*), which share fruit species as their feeding resources in this area (Ávila, Hernandez, & Verlarde, 1996; Lira-Torres, Naranjo-Piñera, Güiris-Andrade, Cruz-Aldán, 2004; González-García, Santana-C, Barbudo, Rico-Gray, & Moliner, 2017).

In the years after the establishment of the reserve, Solórzano, Castillo, Valverde, & Ávila (2000) recorded the number of fruits present in a community of trees producing the feeding resources of quetzals in 1991-1993. The patterns of some tree species observed within this study indicate phenological influences from variable climatic conditions (temperature and rainfall). For example, two species within the wild avocado family Lauraceae, *Nectandra rudis* and *Ocotea chiapensis*, showed patterns of fruit presence which occurred in different months between the two years of study. Other species had seasonal fruiting patterns that did not change greatly in timing between years, indicating possible phenological influences from factors which also do not vary greatly between years (Pau et al., 2011).

In this study we revisited the same area of El Triunfo nearly 30 years later to determine if phenological patterns had changed during this time. Like Solorzano et al. (2000), we focused on the fruits consumed by quetzals (Figure 1), which were the majority of the common tree species producing fleshy animal dispersed fruits in the study area (subsequently referred to as zoochorous community; Figure 1, Table S1). As climate trends occur, changes in the timing of flower and fruit production of some tree species may cause shifts in the overall phenological patterns of this community.

Climate seasonality can be less distinct in tropical mountain environments, where high humidity continues throughout the year from fog and orographic rainfall (Loope & Giambelluca, 1998; Bruijnzeel, Mulligan, & Scatena, 2011). However, in the higher elevations of the Sierra Madre, seasonal climatic differences are evident, most notably in rainfall and minimum daily temperatures. Since 1990, there have been significant trends in temperature and rainfall in the Sierra Madre (Wootton, Enríquez, & Navarrete-Gutiérrez, 2021). Within El Triunfo, the wet season has trended earlier in the year and this season has become wetter. The start of the dry season has also trended earlier in the year and rainfall has decreased from October to December, during the transition to the dry season (Wootton et al., 2021). In the higher elevation areas of El Triunfo, minimum daily temperatures have increased, especially in the colder months of January and February, and maximum daily temperatures have decreased (Figure 1).

In addition to yearly climatic influences, extreme weather conditions (e.g., strong winds and hail) could affect short term phenology through the destruction of flowers and fruits (Bustamante et al., 2010; Williams-Linera, Alvarez-Aquino, & Tolome, 2021). Hurricane winds are rare in the Sierra Madre (Tejeda-Cruz & Sutherland, 2005). However, during the study period from 2019-2021, Hurricane Eta hit the west coast of Southern Mexico bringing maximum wind speeds of 124-170 km/hr to the study area between October 31 and November 6, 2020.

The objectives of this study were to (a) determine the seasonal patterns of flower and fruit presence in the zoochorous tree species community; (b) relate these phenological patterns to climatic variables (temperature, rainfall, solar radiation, and daylength); (c) determine changes in seasonal patterns between periods separated by ~30 years, 1992-1993 and 2019-2020; and (d) determine the effect of Hurricane Eta by comparing tree phenological patterns before and after the hurricane.

2. METHODS

2.1 Study area

The study area is located in the central zone of Polygon 1 in the El Triunfo Biosphere Reserve, Chiapas, Mexico (15º 39' 23.8"N, 92º 48' 29.3" W; Figure S1), within a valley at the higher elevations of the Sierra Madre de Chiapas. Phenological observation points were established along four trails within the valley, mountain crests, and the higher elevation Pacific coastal slope of this area (Figure S1). These trails range in elevation between 1970 and 2100 m a.s.l. where forest composition and diversity vary greatly among riparian, sheltered, and higher wind exposed areas (Breedlove, 1981; Long & Heath, 1991; Solórzano, 1995).

Six climate variables, linked to phenological patterns in other wet tropical forests (Pau et al., 2020; Azad, Kamruzzaman, Paul, Ahmed, & Kanzaki, 2020), were included in this study. These were average monthly minimum daily temperature (Tmin), average monthly temperature (Tmean), average monthly maximum daily temperature (Tmax), monthly rainfall, daylength, and solar radiation. Monthly solar radiation was estimated using the Hargreaves-Samani temperature-based model (Hargreaves & Samani, 1985).

In the study area, Tmin is lowest during December to February (6 ºC) and highest during June (12 ºC). Tmax is less variable throughout the year and range from 23 ºC in January to 25 ºC in May. Rainfall is greatest during June (600 mm) with another peak in September (550 mm), and lowest (100 mm or less) during December to April (Figure 2). Daylength is greatest at this latitude during June (13 hr) and least in December (11.3 hr), and solar radiation is greatest during March-April (21-22 $MJm^{-2}day^{-1}$) and lowest during October-January (15-16 $MJm^{-2}day^{-1}$), depending on cloud cover conditions. Temperature and rainfall data were obtained from the automated El Triunfo weather station at 1972 m a.s.l. located at the central camp in Polygon 1 (CONAGUA, 2021).

2.2 Phenological surveys

Phenological surveys took place approximately on the third week of each month included in the study. Observations were done monthly from March 2019 to March 2020 (excluding July and November 2019), and were meant to continue throughout 2020. However, due to pandemic travel restrictions, observations were postponed until December 2020 (the month after hurricane Eta) and continued monthly until May 2021. A total of 162 individual trees, belonging to 21 species were tagged for phenological observations during this time (Table S1).

Phenological observations focused on reproductive phenophases. These were intensity of flower, unripe fruit, and ripe fruit, and number of ripe fruits per tree. Intensity observations were done by estimating the percentage of the crown of each tree surveyed with flowers, unripe fruits, and ripe fruits. These percentages represented intensity scores of 0 (0%), 1 (1-20%), 2 (21-40%), 3 (41-60%), 4 (61-80%), and 5 (81-100%) (Fournier, 1974).

The number of ripe fruits on each tree surveyed was estimated by counting the number of fruits in the entire tree with the use of binoculars. Where the entire crown was not visible or there were large amounts of fruits in the tree, the number of fruits in a portion of the tree, usually one branch, was counted and this number was multiplied by the estimated remainder of the tree. Some species such as *Citharexylum mocinnii* produced large amounts of fruits in bunches. In this case, the average number of fruits was estimated for each bunch and this was multiplied by the estimation of the number of bunches in each tree.

Calculations of overall zoochorous community values of flower, unripe fruit, and ripe fruit intensity were done by adding each individual species intensity index score for each phenophase. Intensity index scores (Fournier, 1974) were calculated by dividing the sum of phenological intensity scores of individual trees of a species by the maximum possible intensity score for the species (number of individuals multiplied by 5). This fraction was multiplied by 100 to obtain a percent. The monthly number of ripe fruits at the community level was calculated by adding the average number of fruits of each species each month.

Community fruit biomass was estimated by adding the average ripe fruit biomass of each species, which was calculated by multiplying the average monthly number of fruits per species by their average single fruit biomass. Average single fruit biomass per species was measured by the average weight of 25 ripe fruits, including seeds. Yearly and half-year periods were separated into March 2019 – February 2020 and December 2020 – May 2021. The March 2019 value was an average of March 2019 and March 2020 phenophase values.

2.3 Statistical analysis

Circular statistics were used to determine the seasonality of each of the observed phenophases. Months with phenological data were converted to angles around a circle, with January converted to 15º and each month after at 30º intervals. The following calculations and tests of seasonality were done in the program Oriana

4.02 (Kovach Computing Services, 2013): (a) the average angle (date) of the distribution of data; (r) the degree of seasonality of the presence of flowers and fruits with a range of 0 to 1 (where 0 is without seasonality with presence of flowers and fruits distributed uniformly during the year, and 1 is very seasonal with all the presence in one month); and the Rayleigh test (z) which is used to evaluate the significance of seasonality.

Correlations between climatic variables (Tmin, Tmean, Tmax, rainfall, daylength, and solar radiation) and phenophases were determined using Spearman correlation coefficients. Correlations were done in the program InfoStat version 2020 (Di Rienzo et al., 2020) for observations recorded between March 2019 – May 2021.

The Watson-Williams test was used to determine significant differences in the mean date of seasonal ripe fruit production between periods separated by ~30 years and half year periods before and after Hurricane Eta. For seasonality comparisons separated by ~30 years we only included those tree species which were observed both in 1992-93 and 2019-21 (Table S1). Fruiting seasonality of two years in the 1990's, February – December 1992 and January – December 1993 (Solórzano et al., 2000), was compared with our observations from March 2019 – February 2020. To compare fruiting seasonality before and after Hurricane Eta, we included observations from the same months in both periods: April, May and December 2019, January, February, and March 2020 (before period), and December 2020 to May 2021 (after period). A paired sample t-test was used to determine if there were differences in fruit quantities between the periods before and after the hurricane.

3. RESULTS

3.1 Seasonality of flower and fruit presence

During the first observation period (March 2019 – February 2020), trees within the zoochorous community displayed a mean date of highest intensity of flowering on

February 12 (r = 0.55), unripe fruit on December 15 (r = 0.22) and ripe fruit on March 28 (r = 0.37). The mean date of seasonal ripe fruit production (fruit number) was March 12 (r = 0.67) and ripe fruit biomass, which is influenced more by species producing larger fruits (Table S4), was on February 28 (r = 0.56) (Table 2, Figures 3 & 4). During the second period (December 2020 - May 2021), the mean date of highest flowering intensity was March 6 (r = 0.73), unripe fruit intensity January 30 (r = 0.75), ripe fruit intensity April 1 (r = 0.72), ripe fruit number April 8 (r = 0.82), and ripe fruit biomass March 12 (r = 0.66) (Table 2, Figures 3 and 4). All flowering and fruiting patterns were significantly seasonal ($p<0.05$).

Collating the data available (1991-2021), four distinct fruiting patterns can be distinguished: (a) a similar timing of peaks between years (nine species), (b) production of unripe fruits all year long with fruits ripening during multiple times of the year (one species), (c) a distinct peak during the year but the timing of the peak was different between years (three species), and (d) multiple peaks in fruit production throughout the year, but the timing of these peaks differed between years (two species). Six species produced a similarly consistent number of fruits between years, and nine produced inconsistent quantities or had years with no fruit presence (Table 1).

3.2 Relations between climatic variables and phenological patterns

Tree community characteristics of flowering, including number of individuals and species producing flowers per month and monthly flowering intensity, were significantly and negatively correlated with temperature (Tmin and Tmean), daylength, and rainfall (Table S2; Figure 5). The number of trees and tree species producing flowers, and intensity of flowering were highest when Tmin, Tmean, daylength and rainfall were the lowest during the year. These correlations were significant for six of the individual species. For two other species, *Morus insignis* and *Ocotea chiapensis*, flower presence was negatively correlated with solar radiation (Table S3).

The number of species with unripe fruits was negatively correlated with Tmin, Tmean, Tmax and daylength; with fruit presence highest when these variables were lowest during the year. Intensity of unripe fruiting in this community was correlated negatively with Tmin, Tmax, daylength and solar radiation (Table S2). Intensity of unripe fruiting of seven species within this community were individually correlated with these climatic variables; whereas unripe fruit intensity of *Nectandra rudis* (marginally, p=0.07) and *Trophis cuspidata* were positively, and *Morus insignis* and *Citharexylum mocinnii* negatively correlated with monthly rainfall. *Prunus brachybotrya* and *Ardisia verapazensis* were negatively correlated with solar radiation (Table S3).

Ripe fruit presence was positively correlated with solar radiation. This included the number of trees and species with ripe fruits, intensity of fruiting, and number of fruits. Only the biomass of fruit was not significantly correlated with solar radiation (p=0.14). Seven species showed positive correlations between intensity of fruit presence and solar radiation; however, one species showed a negative correlation, and there were various other significant correlations between individual species' ripe fruit presence and temperature, rainfall and daylength variables, both positive and negative (Table S3). There were also significant correlations between individual species' fruit biomass and climatic variables, unlike with the overall community relations (Table S3).

3.3 Seasonality differences after 30 years, and before and after Hurricane Eta

Including only the 17 species which were observed in both our and Solórzano et al. (2000) studies, the mean date of ripe fruit production (mean angle ± SD, r) was March 12 in 2019-20 (71±52, 0.67), March 21 in 1992 (79±77, 0.40) and May 4 in 1993 (122±70, 0.47). Mean dates of fruit estimations were significantly different between both 2019-20 and 1992 (Watson-Williams F = 448, p<0.01), and 2019-20 and 1993 (Watson-Williams F = 14261, p<0.01). Of the species which produced fruits in all of the observation years, five had earlier mean dates of seasonal fruit production in 2019-20 than in 1992 or 1993, whereas nine species had later or similar mean dates (Table 3).

The mean date of number of ripe fruits estimated during the December – May half year period before Hurricane Eta was March 7 (66±39, 0.80) and after was March 24 (83±26, 0.90). Mean dates of seasonal fruit production during these periods before and after Hurricane Eta were significantly different (Watson-Williams F = 4995, $p<0.01$), and there was a significant difference in community fruit number between the periods before (9339±5535) and after (2423±2493) the hurricane (t (5) =-2.79, $p=0.02$).

4. DISCUSSION

Our results suggest that yearly variation in rainfall and temperature, long-term climate trends, and extreme weather events are affecting phenological patterns within the cloud forest of the Sierra Madre in Chiapas, Mexico. Cloud forests have distinct climatic conditions within tropical areas (Hu & Riveros-Iregui, 2016) and some climate trends have been different in the higher elevations of the Sierra Madre than in the lower elevation forests (Wootton et al., 2021). High endemic tree species diversity of both temperate and tropical origin (González-Espinosa et al., 2011) is another distinct characteristic of these ecosystems which could influence phenological responses to climate changes (Borchert, Robertson, Schwartz, & Williams-Linera, 2005). This shows the importance of recent and ongoing phenological information from these tropical mountain ecosystems which are the reproductive habitats of many endemic frugivores.

4.1 Phenological patterns in the cloud forest of El Triunfo

Peaks in ripe fruit presence occurred during the end of the dry and beginning of the wet seasons between 2019-21. This pattern contrasted with the majority of community fruit peaks in the lower elevation tropical rainforests of the Neotropics, which often occur during the wet season (Mendoza et al., 2017), when germination success and seedling survival can be greater (McLaren & McDonald, 2003).

However, in comparison with fruiting patterns in other Mesoamerican cloud forests, this was similar to seasonal patterns in the same area 30 years earlier (Solórzano et al., 2000), and in the Cordillera de Talamanca, Costa Rica (Camacho & Orozco, 1998). Two peaks during the year were recorded in Veracruz, Mexico during the dry-warm and wet-warm times of the year (Williams-Linera, 1997) and in Costa Rica during the dry and wet periods (Dinerstein, 1986).

Cloud forests have some unique characteristics and conditions which may influence community fruit production patterns. These include a high diversity of endemic tree species (Williams-Linera, 2002), animal dispersers of fruit which migrate altitudinally throughout the year (Boyle, 2010), and a longer duration of humidity and water availability from cloud cover which could also influence solar radiation (Jarvis & Mulligan, 2011). Cloud forests also receive some of the largest quantities of rainfall in Mexico, which in the Sierra Madre, has been increasing at a greater rate than the adjacent lower elevation regions (Wootton et al., 2021). Fruit ripening peaked just before the wettest period began, when solar radiation was highest, and after a period of flower production during the time of the year when Tmin was lowest. It was also highest during the reproductive season of the quetzal which may increase the potential for seed dispersal (Wheelwright, 1983).

In addition to climatic influences, various tree species within the zoochorous community showed phenological characteristics influenced by biotic interactions. *Ardisia compressa* continuously produced fruits, which may be a strategy to disperse seeds throughout the year by a specialized animal disperser (Van Schaik et al., 1993). The distinct seasonal peaks in ripe fruits, shown by eight species, may be linked to the arrival times of a migratory dispersal animal such as the quetzal (Solórzano et al., 2000), or spider monkey (González-Zamora et al., 2009).

Ocotea chiapensis produced various peaks in ripe fruit throughout the year. This may be important for food availability for animals which stay year-round in the cloud forest, during the summer wet season when fruit is scarcer in this forest.

Most of the species produced a large number of fruits one year and a low amount or no fruits the next year. These included the species in the Lauraceae family which Wheelwright (1986) suggested was a strategy to allocate resources between reproduction and vegetative growth between years. We also observed year-round fruit presence in another common species in the cloud forest, *Glossostipula concinna*, which produce harder and larger fruits than quetzals consume, but are eaten and distributed by animals after they break apart the fruit.

4.2 Climatic influenced flowering and fruiting patterns

Community flower presence mainly occurred during the months of the year with the lowest temperatures and daylength (January – March), although in 2021 there was also high flower presence in April which is a warmer month. Tmin is the temperature variable which changes greatest throughout the year in the study area, and flower presence was significantly (negatively) correlated with this. Ramírez & Davenport (2016) discussed that some species within tropical regions which are related to species in temperate regions such as *Prunus* sp. may require a dormant period during cooler temperatures to initiate flower production. Community flowering was greatest during the driest part of the year (January - April), which may coincide with a higher abundance of pollinators and lower potential for storm damage (Van Schaik et al., 1993; Xu & Servedio, 2021).

Unripe fruit presence was also negatively correlated with temperature and daylength, as well as solar radiation. The development of unripe fruits is dependent on the timing of flowering patterns, so the climatic correlations with the fruit development period may be due more to flowering times (Bendix et al., 2006). Unlike flowering, unripe fruit intensity and rainfall were not correlated. This may be related to the lower seasonality of unripe fruit presence which lasts throughout both the dry and wet periods.

Community ripe fruit presence was significantly positively correlated with solar radiation for number of trees and number of species producing fruits, intensity of fruiting, and number of fruits produced. Solar radiation is an important factor influencing plant transpiration (Turc, 1961), which increases water and nutrient flow through the tree (Montanaro, Dichio, & Xiloyannis, 2010) and can influence fruit development (de Azevedo, de Souza, da Silva, & da Silva, 2007). It also has been shown to be directly an important factor in fruit ripening in other tropical forests (Chapman, Valenta, Bonnell, Brown, & Chapman, 2018). We estimated solar radiation at the site of the El Triunfo weather station based on extraterrestrial radiation and daily temperature range, which indicates cloud cover and atmospheric transmittance of radiation (Quej et al., 2016). The actual solar radiation affecting each tree observed could vary from this estimation due to local factors such as cloud and fog cover, slope aspect, and forest canopy conditions. These conditions change greatly throughout the valleys and slopes of the study area and between species heights.

Some tree species showed correlations between a characteristic of flower or fruit presence and climatic variables which were different from the overall community correlations. These species correlations may be related more to the duration of the ripe fruit production period, although some species had peaks in fruiting during the wettest period of the year. There was also high variation within populations of species in timing of fruit presence. Community patterns may be due to individual tree patterns rather than species composition (although some species such as *Morus insignis* had high synchronization between individuals and seasonality). Therefore, climatic factors may be affecting the tree community patterns independently from individual species phenological behaviours.

4.3 Effects of climate trends and hurricane winds on phenological patterns

Between 1990 and 2020, Tmin increased and Tmax decreased in El Triunfo (Wootton et al., 2021). Rainfall patterns shifted earlier in the year: the start and end of the wet season trended earlier in the year and rainfall peaks shifted from late in the wet season (September) to early (June). These changes in temperature and rainfall seem to have influenced the earlier shift in the overall seasonal patterns of zoochorous community fruit presence between 1992-93 and 2019-20, although this was variable amongst species.

Warmer and wetter trends have also been recorded in areas with longer term phenological observations in Africa. In Uganda, Chapman et al. (2005) determined that as these climate trends occurred, a higher proportion of trees produced fruits, but some species rarely produced fruits in the later years. We observed little fruit presence in some species during 2019-21 such as *Symplococarpun purpusii*, although this species seems to produce fruits every second year so differences may be due to this interannual variability. Fruit production also increased greatly between 1992-93 and 2019-20 in two of the most common Lauraceae species in El Triunfo *Ocotea chiapensis* and *Nectandra rudis*.

Increasing rainfall trends have also been linked to the number of species with fruits and timing of fruiting within tropical tree communities. Dunham et al. (2018) recorded a higher richness of species producing fruits and a greater intensity of fruiting in Madagascar during a period of increasing rainfall. In this area, after dry seasons receiving less rainfall than normal, there was a later shift in fruiting patterns in the next year (Dunham et al., 2018). 1990 and 1991 were exceptionally dry years in Chiapas and around the world (Murray-Tortarolo, Jaramillo, Maass, Friedlingstein, & Sitch, 2017). This drought may have influenced the later fruiting patterns observed in 1992-1993 in El Triunfo, than in 2019-21.

Changes in air temperature may have also affected fog conditions. Solórzano et al. (2000) described months during their phenological observations when it was not possible to count fruits due to heavy fog. But there were no months during our observations when fog was so thick that fruits could not be observed. Less fog cover could increase the amounts of solar radiation reaching the forest and decrease available water during the dryer period of the year (Giambelluca, DeLay, Nullet, Scholl, & Gingerich, 2011). This may have influenced the higher seasonality of ripe fruit in comparison to 1992-93 (Table 2), with peaks in March and April before increased cloud cover during the wet season would have resulted in decreased solar radiation reaching the forest canopy.

The length of ripe fruit presence in the trees may also have been related to frugivore abundance. The timing of fruiting coincided with the reproductive period of many frugivore species in El Triunfo (Ávila et al., 1996; González-García et al., 2017), when fruit consumption needs are greater (Ávila et al., 1996). The large quantities of ripe fruits eaten during this time could also be part of the reason for the more intense seasonality recorded in recent years, as increased conservation efforts since El Triunfo's establishment in 1990 may have increased the abundance of frugivores in this area.

For the observation period after Hurricane Eta, seasonality values are only indicators of half-year patterns so cannot be directly compared to the full year of observations in 2019-2020. But they do show the variation in seasonal patterns between phenophases during this period when the greatest production of fruit occurs. In the month after the hurricane, we observed that many larger trees had fallen, including some tagged trees from our study. Strong winds may have caused flowers and unripe fruits to fall, disrupting the patterns of ripe fruit production, and lowering the number of fruits present in the zoochorous community. This reduction in community fruiting is similar to what occurred after Hurricane Karl in Veracruz, Mexico (Williams-Linera et al., 2021). The production of flowers once again after this wind event may have resulted in a later ripe fruit development in comparison to earlier years.

4.4 Ecological implications for the El Triunfo Biosphere Reserve

Shifts in phenological patterns related to climate trends demonstrate changing ecological conditions within the cloud forests of a nationally protected area. Some of the factors influencing climate trends in the Sierra Madre since 1990 are cyclical over longer time periods (Méndez-González, Ramírez-Leyva, Cornejo-Oviedo, Zárate-Lupercio, & Cavazos-Pérez, 2010; Fuentes-Franco et al., 2015), so their effects on fruit production patterns during the next 30 years may be different than the past 30 years. However, severe weather events such as tropical storms and droughts are expected to occur more frequently in the next decades in Mexico (Murray-Tortarolo et al., 2021), and as shown in the results of our study, can have drastic effects on fruit production. Our results suggest that climate trends have influenced shifts in the timing and seasonality of fruit production, whereas an extreme weather event affected numbers of fruits produced; both conditions having long and short-term consequences for fruit availability in the reserve.

ACKNOWLEDGEMENTS

We thank Marco Domínguez for his contribution to the field observations, Rubén Martínez for help with tree species identification, and to the directors, managers, and park rangers of the El Triunfo Biosphere Reserve for their help with species identification and field logistics. The first author received a CONACyT doctoral scholarship (No. 884660). Field work in El Triunfo received permission from CONANP and fruit collection from SEMARNAT (No. SGPA/DGVS/8055/19).

AUTHOR CONTRIBUTION

AW, PE and GW conceived the study and analysis, AW collected field data and did the analysis, and EP assisted with data organization and analysis. AW wrote the manuscript with revision from PE, GW and EP.

DATA AVAILABILITY STATEMENT

Field data are available on request.

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Table 1. Ecology and phenology of the quetzal's feeding resources trees in the cloud forest of El Triunfo.

Species	**Ecology**	**Location in the canopy**	**Fruiting peak**	**Duration of peak**	**Fruiting pattern**	**Consistent production between years**
Eugenia capuli	slopes & ravines	understory	Dec	short	distinct peak & same timing between years	no
Conostegia volcanalis	slopes & ravines	understory	Feb/May	long	distinct peak but not consistent between years	yes
Hedyosmum mexicanum	wet & disturbed areas	understory	Mar-May	long	distinct peak & same timing between years	yes
Trophis cuspidata	Slopes	understory & codominant	Sept	short	distinct peak & same timing between years	no
Ardisia compressa	slopes & ravines	understory & codominant	Throughout Apr-Oct	long	unripe fruits all year, various peaks in ripe fruits in different times of the year & between years	yes
Symplococarpun purpusii	slopes & secondary	understory or codominant	Feb or none	short	distinct peak but not consistent between years	no
Saurauia madrensis	slopes & ravines	understory or codominant	May	long	distinct peak & same timing between years	yes
Prunus brachybotrya	slopes & ravines	codominant	Jan	long	distinct peak & same timing between years	yes
Citharexylum mocinnii	slopes	codominant	Feb-Apr	long	distinct peak but not consistent between years	no
Frangula capreifolia	secondary	codominant	Jun	short	distinct peak & same timing between years	yes
Morus insignis	slopes & ravines	codominant	Feb-Mar	short	distinct peak & same timing between years	no
Licaria excelsa	slopes & ravines	codominant	Dec-Jan	long	peaks throughout the year, but not same timing between years	no
Cinnamomum zapatae	Slopes	codominant	Mar	short	distinct peak & same timing between years	no
Ocotea chiapensis	slopes and valley bottom	dominant	Throughout year	long	peaks throughout the year, but not same timing between years	no
Nectandra rudis	slopes and valley bottom	dominant	Dec	long	distinct peak but not consistent between years	no

Table 2. Characteristics of seasonality of flower, unripe fruit, and ripe fruit production during 1992, 1993, and 2019-2021 in El Triunfo, Mexico.

Phenophase	**Mean angle**	**Date**	**Vector r**	**Rayleigh z**
February-December 1992 (Solórzano et al. 2000)				
No. ripe	87	March 29	0.332	6684.2
January-December 1993 (Solórzano et al. 2000)				
No. ripe	122	May 4	0.489	9267.0
March 2019-February 2020				
Intensity flower	42	February 12	0.553	271.3
Intensity unripe	344	December 15	0.222	63.4
Intensity ripe	86	March 28	0.367	291.2
No. ripe	70	March 12	0.666	28983.2
Biomass	57	February 28	0.564	31914.2
December 2020-May 2021				
Intensity flower	64	March 6	0.729	430.5
Intensity unripe	30	January 30	0.753	556.4
Intensity ripe	90	April 1	0.716	465.9
No. ripe	97	April 8	0.816	9685.9
Biomass	70	March 12	0.656	8164.5

Table 3. Phenological circular statistics of eleven tree species during the yearly cycles: February – December 1992, January – December 1993 (Solórzano et al., 2000), and March 2019 – February 2020 (this study). Variables are number of trees observed in each study (n), degree of seasonality (r), significance of seasonality (z), average angle of the distribution of the data (angle) and the day of the year corresponding to this angle (date).

Variable	Year	n	r	z	Angle	Date
Ardisia compressa	1992	16	0.55	100	175	Jun 26
	1993	16	0.91	286	70	Mar 12
	2019	6	0.48	105	149	May 31
Cinnamonum zapatae	1992	6	0.98	13285	63	Mar 5
	2019	3	0.99	1069	71	Mar 13
Citharexylum mocinnii	1992	5	0.44	1389	161	Jun 12
	1993	5	0.52	2748	113	Apr 25
	2019	7	0.82	33560	71	Mar 13
Conostegia volcanalis	1992	11	0.48	448	112	Apr 24
	1993	11	0.80	914	127	May 9
	2019	8	0.70	1190	76	Mar 18
Eugenia capuli	1992	5	0.60	45	333	Dec 4
	1993	5	0.92	245	338	Dec 9
	2019	15	0.78	113	332	Dec 3
Frangula capreifolia	1992	5	0.69	5019	185	Jul 7
	1993	5	0.81	8639	151	Jun 2
	2019	4	0.98	3130	157	Jun 8
Licaria excelsa	1992	5	0.33	471	1	Jan 1
	1993	5	0.61	684	138	May 20
	2019	7	0.82	188	12	Jan 12
Morus insignis	1992	11	0.96	985	58	Feb 28
	1993	11	0.98	3497	57	Feb 27
	2019	8	1.00	781	77	Mar 19
Nectandra rudis	1992	9	0.83	44	49	Feb 19
	1993	9	0.25	14	318	Nov 18
	2019	15	0.74	512	358	Dec 29
Ocotea acuminatissima	1992	5	0.56	30	57	Feb 27
	1993	5	0.84	186	61	Mar 3
	2019	5	0.97	30	29	Jan 29
Ocotea chiapensis	1992	40	0.75	7	58	Feb 28
	1993	40	0.26	3	51	Feb 21
	2019	15	0.23	57	70	Mar 12
Prunus brachybotrya	1992	6	0.69	6459	45	Feb 15
	1993	6	0.74	988	24	Jan 24
	2019	13	0.67	3279	32	Feb 1
Saurauia madrensis	1992	5	0.59	29	193	Jul 15
	1993	5	0.91	64	116	Apr 28
	2019	4	0.79	584	113	Apr 25
Trophis cuspidata	1993	5	0.95	1400	297	Oct 28
	2019	15	0.52	506	253	Sep 14

Figure 1. Photos of the 21 tree species included in this study which produce the feeding resources of the quetzal in the cloud forest of polygon 1 of El Triunfo, Mexico. Species shown are: (1) *Ocotea chiapensis*, (2) *Nectandra rudis*, (3) *Licaria excelsa*, (4) *Ocotea acuminatissima*, (5) *Cinnamomum zapatae*, (6) *Saurauia madrensis*, (7) *Saurauia yasicae*, (8) *Conostegia volcanalis*, (9) *Citharexylum mocinnii*, (10) *Hedyosmum mexicanum*, (11) *Ardisia compressa*, (12) *Ardisia verapazensis*, (13) *Morus insignis*, (14) *Trophis cuspidata*, (15) *Frangula capreifolia*, (16) *Symplococarpun purpusii*, (17) *Dendropanax arboreus*, (18) *Clusia salvinii*, (19) *Prunus brachybotrya*, (20) *Prunus tetradenia*, (21) *Eugenia capuli*.

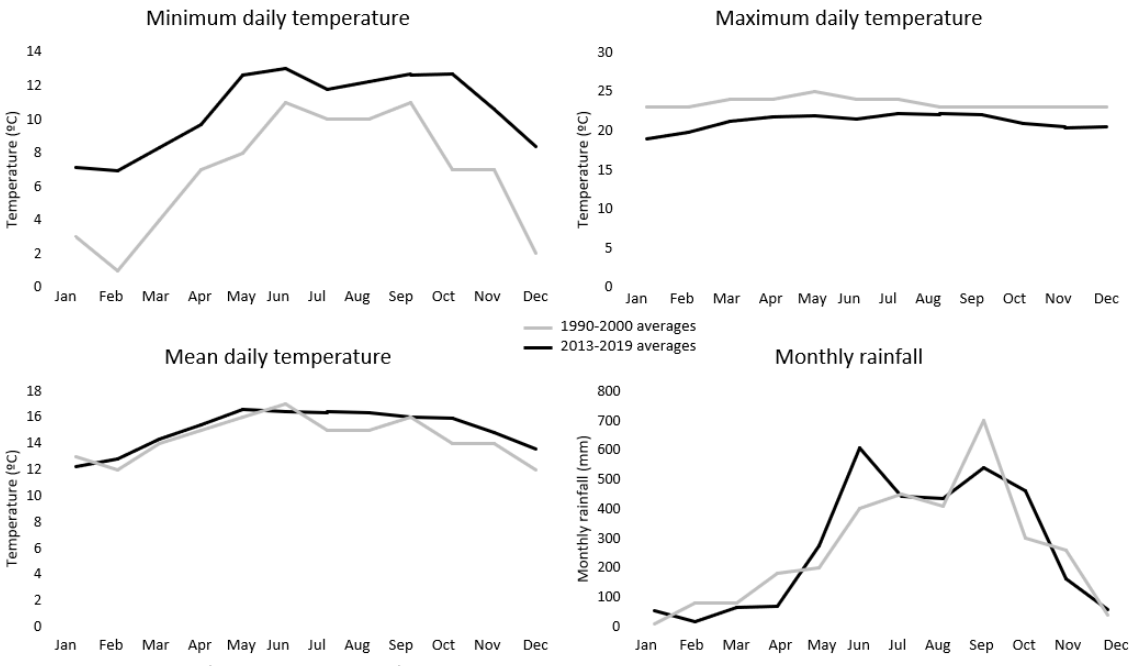


Figure 2: Average minimum, mean and maximum daily temperatures and monthly rainfall during the 1990-2000 (Solórzano et al., 2010) and 2013-2019 (CONAGUA, 2021) periods in El Triunfo, Mexico.

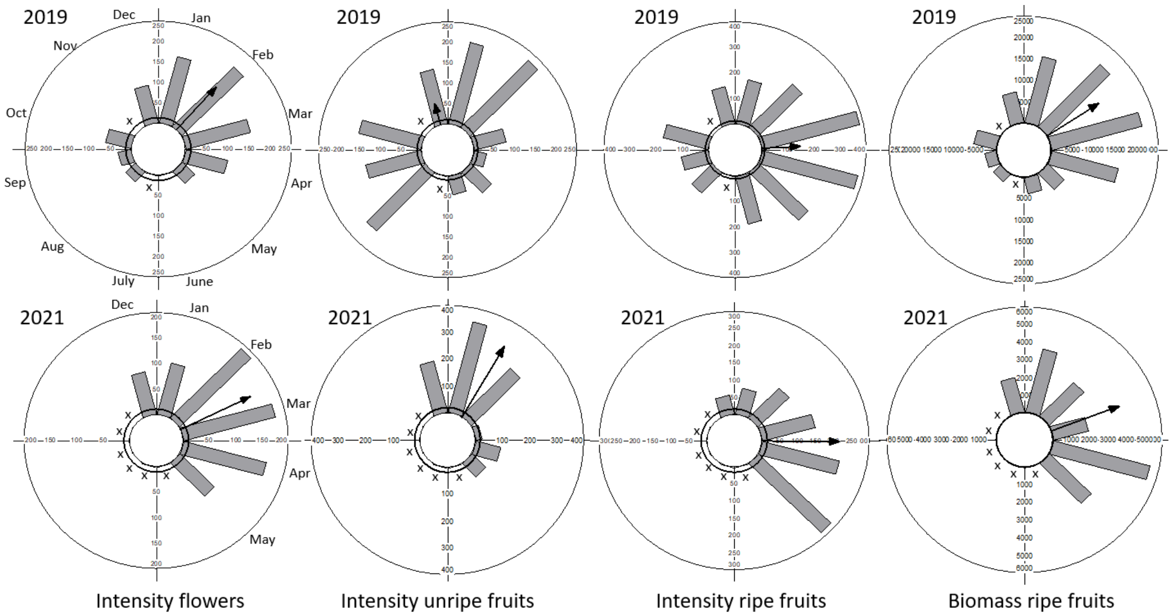


Figure 3. Circular histograms of flower, unripe fruit and ripe fruit intensity and ripe fruit biomass in the community of the quetzals feeding resources during March 2019-February 2020 (2019), and December 2020 – May 2021 (2021). Months without observations are shown with an x. Arrows indicate the degree of seasonality (r value). Numbers in intensity histograms are the sums of intensity scores for each species and numbers in biomass histograms are the sum of estimates of total biomass (g) for all trees observed in the study.

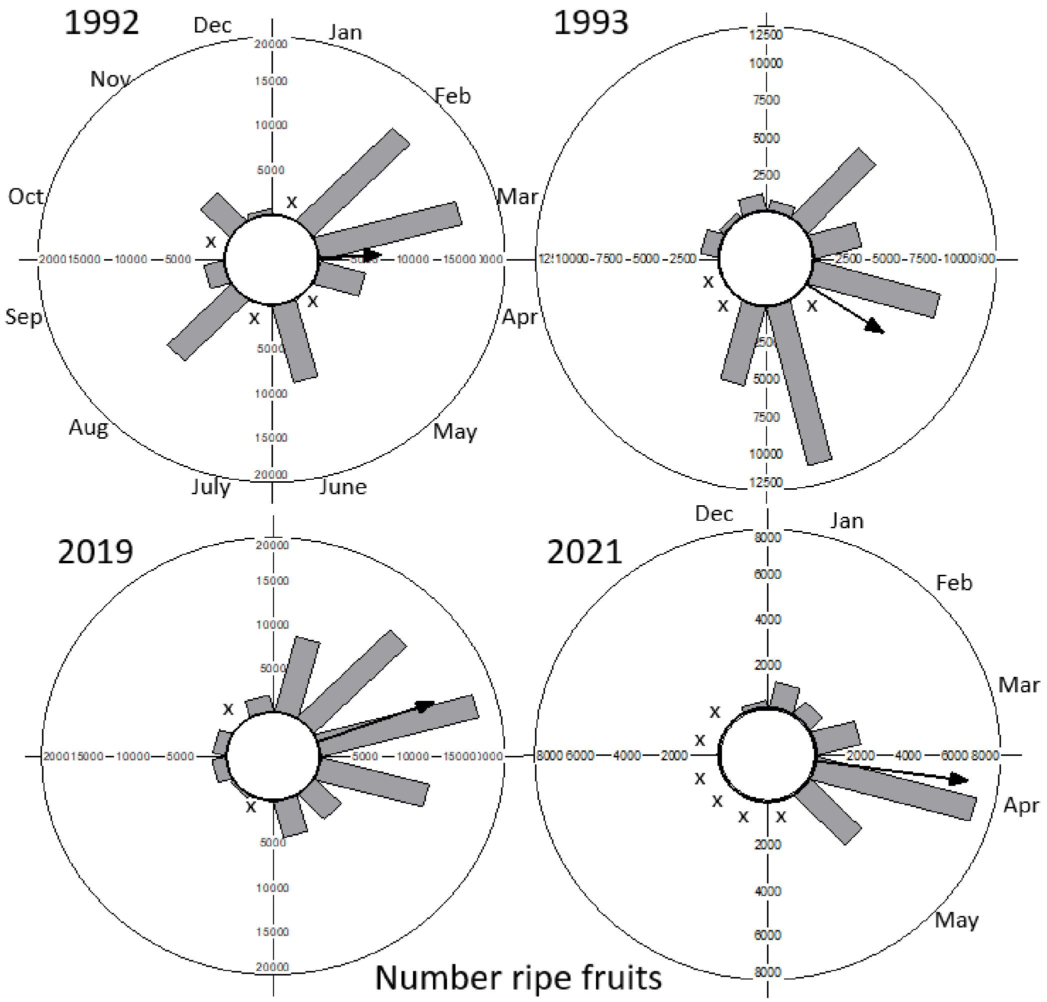
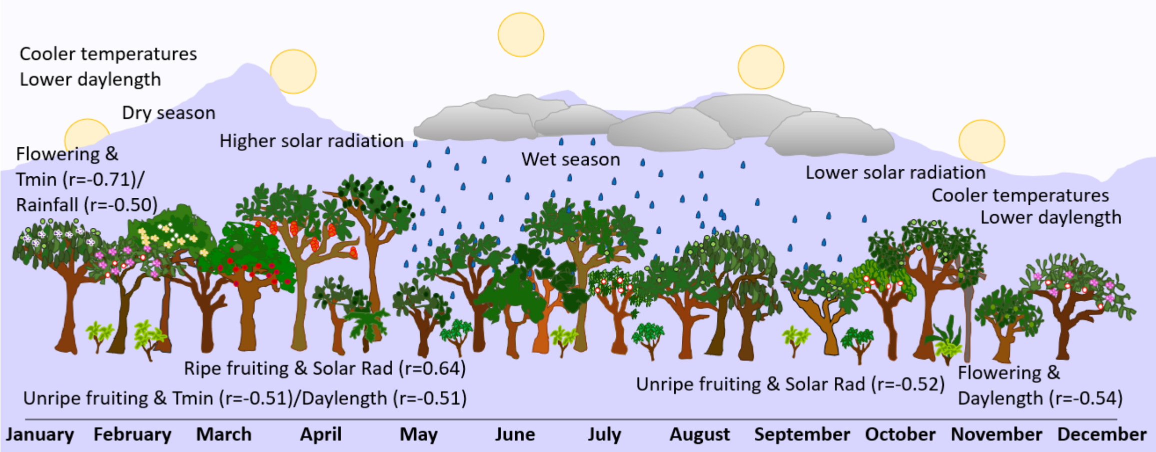


Figure 4. Circular histograms of number of ripe fruits in the tree community of the quetzals feeding resources during: (1992) February - December 1992, (1993) January-December 1993 (Solórzano et al., 2000), (2019) March 2019-February 2020, and (2021) December 2020 – May 2021. Months without observations are shown with an x. Arrow length indicate the degree of seasonality (significant r value; Table 2). Numbers in histograms are number of ripe fruits estimated monthly in all trees observed.

Figure 5. Significant (p<0.05) correlations between yearly climatic variables and phenophases of the zoochorous community in the cloud forest of El Triunfo, Chiapas. Numbers within parenthesis are Spearman Correlation coefficients; Solar Rad is solar radiation, and Tmin is minimum daily temperature.



CAPÍTULO 4

Hábitat reproductivo del quetzal, Sendero Cerro El Triunfo. Foto de Allen Wootton.

Spatial and temporal relations between fruit production, tree species composition and quetzal abundance within a Mexican cloud forest*

Abstract

Throughout Mesoamerica, quetzals (*Pharomachrus mocinno*) migrate altitudinally following seasonal fruit availability. It is less known, however, how long-term changes in fruiting phenology affect quetzal abundance patterns, and how these patterns relate to fruit availability and tree species composition within their cloud forest reproductive habitat. We aimed to determine: (1) the long-term seasonality of quetzal abundance at higher elevations, (2) if this was related to fruiting and rainfall patterns, (3) the spatial relations between quetzals and habitat characteristics within the cloud forest, and (4) the tree species composition of this habitat in El Triunfo Biosphere Reserve, Mexico. Data was collected from monthly quetzal and fruit number observations, and tree composition plots; and analyzed using circular statistics, correlations, and a dissimilarity index. The average date of seasonal quetzal presence in the cloud forest from 2010-2020 ranged between January and April. Overall monthly quetzal abundance was positively correlated with community fruit production, biomass of fruits, and number of species with fruits. Local quetzal abundance (within 3 ha) was spatially correlated with tree species diversity, number of Lauraceae trees, biomass of Lauraceae fruits, and stream distance. Our results suggest that habitat variables influence quetzal abundance and distribution in the El Triunfo cloud forest.

Key words

El Triunfo, feeding resources, frugivorous populations, reproductive habitat, seasonal migration

*Artículo en preparación para enviar al Journal of Tropical Ecology
https://www.cambridge.org/core/journals/journal-of-tropical-ecology

Introduction

The spatial and temporal abundance of quetzals (*Pharomachrus mocinno*) is strongly related to the availability of fruits (Solórzano et al. 2000, Bustamante et al. 2010), similarly to other tropical mountain frugivores including cassowaries in Papua New Guinea (Wright 2005), and other birds in the neotropics (Loiselle & Blake 1993). Long-term changes in forest cover (Castro-Hernández 2019, Wootton et al. 2021a), and fruit production patterns (Wootton et al. 2021b) in the Sierra Madre de Chiapas, Mexico, may be influencing the abundance patterns of quetzals (Gasner et al. 2010, Potts et al. 2020) in their cloud forest reproductive habitats of this region.

In the 1980's, Wheelwright (1983) reported that quetzal's altitudinal migration in the mountains of Costa Rica follows the availability of fruits produced from tree species in the Lauraceae family. In the early 1990's in the cloud forest of Chiapas, Mexico, correlations were reported between quetzal abundance and the monthly number of tree species producing the fruits consumed by the quetzal, and overall fruit production in this community (Solórzano et al. 2000). However, quetzal abundance and fruit production from Lauraceae species were not correlated (Solórzano et al. 2000), despite these fruits comprising a large part of the diet for quetzal chicks in this area (Ávila 1996).

In the 2000's, quetzals were observed to be more abundant at different elevation ranges at times with higher fruit production at these elevations in Guatemala (Bustamante et al. 2010) and at higher elevations in Costa Rica (García-Rojas 2006); although in this latter location, abundance was greater at higher elevations even when there was a greater fruit production at lower rainforest elevations. Thus, besides overall fruit production, other factors may be contributing to the migration of quetzals to their higher elevation reproductive habitats during a certain period of the year. The factors include lower nest predation (Boyle 2008), nesting trunk availability (Renner 2005), or more nutritious fruits (Carleton & Smith 2016). Rainfall patterns can also influence altitudinal migration to lower elevations, during periods of heavy rainfall at higher elevations (Boyle 2017). In addition to altitudinal migration, like other frugivores, quetzals may migrate and be more locally abundant within parts of their cloud forest reproductive habitat due to the distribution and composition of feeding resource tree species (Kattan & Valenzuela 2013, Pontes et al. 2020). One area where this may be occurring is in the El Triunfo Biosphere Reserve, Mexico.

El Triunfo was established in 1990 to protect the high diversity of flora and fauna in the Sierra Madre de Chiapas, Mexico. The reserve includes five polygon areas of higher protection. The higher elevation region of polygon 1 is an important reproductive habitat for quetzals (Ávila et al. 1996). In this area, the diet of the quetzal (Ávila et al. 1996) and feeding resource availability in relation to quetzal abundance (Solórzano et al. 2000) were studied previously during the 1980's and 90's. In 2010, the monitoring of priority animal species program began in the reserve, which involved monthly records of the abundance of seven animal species, including quetzals (CONANP 2020). These records provide important data on the multi-year cycles of population abundance, to help determine how these vary over a longer period, and to see if long term changes in fruiting patterns could affect the relationship between fruit availability and quetzal abundance. Long term abundance records can also show how the distribution of quetzals is related to habitat characteristics in their reproductive area.

An important characteristic of the quetzal's reproductive habitat is a high diversity of forest structure and tree species composition (Renner 2005, Carleton & Smith 2016). In Mexico, cloud forests are often broadly known and mapped as *bosque mesófilo de montaña* (Rzedowski 1996). However, due to the complex topography, climate, and high diversity of tree species in tropical mountains, cloud forests contain a heterogeneous matrix of forest types within a small geographical area (Martínez-Camilo et al. 2018, Williams-Linera et al. 2013). In Chiapas, Breedlove (1981) distinguished between the higher wind exposed areas (*Elfin forest*) and more sheltered valleys of the cloud forest. Long and Heath (1991) also made this distinction in polygon 1 of El Triunfo based on the dominant species within forest types of this area.

Various studies have reported the relations between forest characteristics and the distribution of quetzals. For example, Solórzano (1995) described a higher abundance of quetzals in ravines and a low abundance in the wind-exposed *Elfin forest* in El Triunfo. In Costa Rica, Carleton & Smith (2016) recorded that highly nutritious fruits of the Lauraceae family comprised a large proportion of the fruits from nearby trees brought to newborn quetzals by their parents. Tree species of this family may be more abundant in certain topographical conditions (e.g., crests or valley bottoms) of the mountain forest, but this could depend on the species (Sri-Ngernyuang et al. 2003). Additionally, stream location can also influence tropical bird distribution within their habitat because of greater feeding resource abundance (Chan et al. 2008) and water sources (Pangau-Adam et al. 2015).

Therefore, differences in tree species composition and physical conditions within the cloud forest may influence the spatial abundance of quetzals. This can be due to temporal changes in fruit availability, which are related to spatial patterns of tree community structure and species composition (Worman & Chapman 2006). The relations between quetzals and phenological and distribution characteristics of tree species could have conservation implications for the quetzal, as forest fragmentation or restoration, stream diversion, hurricanes, fires, and landslides could all affect forest composition landscape patterns and habitat suitability (Gomes et al. 2008, Solórzano et al. 2003, Tejeda-Cruz & Sutherland 2005).

Our objectives were to determine (1) seasonal abundance patterns of quetzals in their reproductive habitat of the cloud forest of El Triunfo from 2010-2020; (2) correlations between the overall abundance of quetzals in the cloud forest, and feeding resource and rainfall variables which could explain this; (3) the spatial relations between quetzal abundance, and feeding resource tree composition and fruit production within the cloud forest; and (4) the characteristics of tree species composition groups which could affect quetzal distribution within this forest.

Methods

Study Area

The study, and ongoing quetzal abundance monitoring, took place in the central zone of Polygon 1 of the El Triunfo Biosphere Reserve in Chiapas, Mexico (Figure 1). The study area is mainly within a mountain valley, and includes the higher elevation crests of the valley and part of the Pacific coastal side of the mountain. This area is an important reproductive habitat of the quetzal at the higher elevation range of its migration routes in the cloud forest of the Sierra Madre.

Dominant trees include species of oaks at higher elevations in the valley, and a higher diversity of species in the valley bottoms. Along riparian areas, dominant species are *Hedyosmum mexicanum*, *Conostegia volcanalis*, and *Eugenia capuli*. Large trees in the Lauraceae family are also often located in the wetter valley bottoms (pers. obs.). The valley once contained a larger extent of cleared land for agriculture, but much of this has grown into secondary forest since the establishment of the reserve in 1990 (Castro-Hernández 2019).

Monitoring of quetzals was done along various lengths of the six trails of polygon 1, Finca Prusia: 0-3000m, Palo Gordo: 0-3000m, Costa: 0-3000m, Bandera: 0-3000m, Monos: 0-2500m, and Cerro El Triunfo: 0-1500m. Fifty-three plots were also done along these sections of trail. Plots were 150m long and 10m wide, and the end of one plot and beginning of the next were separated by 150 m along the trails (Figure 1). Plots ran along the left side of each trail in the direction away from the central camp. These were done only on one side of the trails because the forest structure and composition were similar on both sides of the trail in steeper areas. In flatter riparian areas, forest structure and composition were sometimes different on each side of the trail, but the stream and riparian vegetation type crossed the trail at various points, so these were represented within the plots.

Due to topography and wind direction, daily weather patterns are diverse throughout the study area. Winds and fog cover are greatest at the higher valley crests, and fog and rainfall are often variable throughout the day and location. The wettest period of the year is between April and November, and moisture also arrives to the forest throughout the year in the form of fog. Rainfall data were obtained from the El Triunfo weather station in the study area (CONAGUA 2021).

Quetzal abundance monitoring

Quetzal abundance surveys began in January 2010 in polygon 1 of El Triunfo as part of the monitoring project of priority species established by the reserve (CONANP 2020). We joined these surveys in May 2018 and continued for an additional 17 consecutive and nonconsecutive months during quetzal feeding resource observations (Wootton et al. 2021b). These surveys continued during approximately the third week of each month. Surveys began at 7:00 a.m., and the abundance of quetzals was recorded by sight or sound by walking along the six trails of Polygon 1 at a rate of 1 km/hr. Markers were placed at 50 m intervals along the trails up to 3 km to ensure this monitoring rate. A total of 16 km of surveys took place each week in the six trails included in the monitoring.

Seasonal quetzal abundance analysis included full-year data of overall quetzal abundance (number of quetzals/16km) from 2010-2020. Local quetzal abundance was calculated as the number of quetzals per hectare within 150 m of a plot centre along the trail and 50 m perpendicular to each side of the trail (3 ha segments). The number of quetzals/ha in these locations in relation to forest composition, structure and physical features also included full-year data from 2010-2020, and relations with fruit availability included data from the months where fruit number data were available from 2019-2021 (Wootton et al. 2021b).

Fruit quantity surveys

Data of number of fruits present each month within the tree community of the quetzals feeding resources was obtained from a phenological study described in

Wootton et al. (2021b). Ripe fruits available to be consumed by frugivores were counted/estimated on 162 trees representing 21 species of feeding resources of the quetzal, for 17 months between March 2019 and May 2021. Fruit counts done each month were converted to biomass estimates for each species by multiplying the biomass of the individual fruit by the number of fruits estimated each month. The biomass of an individual fruit of each species was determined by calculating the average weight without seeds of a random sample of 25 collected fresh fruits of each species.

Feeding resource tree species composition measurements

Trees of species producing the quetzal’s feeding resources (SM Table 1) were recorded, and the diameter at 1.3 m (diameter at breast height, DBH) of each of these trees was measured within 53 (0.15 ha) plots located along six of the trails in Polygon 1 (7.95 ha in total; Figure 1). Trees measured within these plots were put into two categories. Category 1 included all trees measured, representing the structure of current and future fruit producing trees. Category 2 included only trees with diameters indicating they were a mature individual that could produce fruits. Diameters of mature trees varied depending on the species and were based on the minimum diameter of the individuals tagged which were observed producing fruits for each species (SM Table 1). This forest composition was used to estimate local fruit availability by adding the individual species variables of average ripe fruit production per tree of each species multiplied by the number of mature trees of each species in each plot.

Statistical analysis

Yearly seasonal patterns of quetzal abundance were determined using circular statistics. First, the months with data were converted to angles around a circle, where January is 15º and the other months continue at 30º intervals. Monthly quetzal abundance at each angle was used to determine the angle (a) corresponding to the mean date of seasonal quetzal presence. The (r) value represents the seasonality of the data where 1 would indicate all quetzals were recorded in only one month of the year, and 0 indicates there are equal numbers of observations during all months of the year (no seasonality). The (z) value represents the significance of seasonality.

Correlations between monthly quetzal abundance and overall habitat variables which could explain their abundance in the cloud forest were done using Spearman correlation coefficients in InfoStat version 2020 (Di Rienzo et al. 2020). These monthly variables were: (1) total number of fruits estimated in the trees tagged for phenological observations, (2) total biomass of these fruits, (3) number of species producing fruits, (4) number of fruits in species of the Lauraceae family, (5) biomass of Lauraceae fruits, and (6) monthly rainfall; during months when fruit number or rainfall data were available (CONAGUA 2021, Wootton et al. 2021b).

Spatial relations between local quetzal abundance and topographic and feeding resource aspects of their habitat were tested using Spearman correlations. Correlations were tested between the total number of quetzals per ha observed within 3 ha from each plot centre during the 17 months of fruit production observations between March 2019 and May 2021 (Wootton et al. 2021b), and four fruit availability variables within each plot. These within plot variables were: (1) estimations of number of fruits present, (2) biomass of these ripe fruits, (3) number of ripe fruits of species in the Lauraceae family, and (4) biomass of these Lauraceae fruits.

Longer term (11 year) spatial relations between quetzal observations from 2010-2020 within the 3 ha segments and topographic and feeding resource aspects of their habitat were also done using Spearman correlations. Habitat variables were based on data collected within each plot. They included: number of trees/ha (for category 1 and 2 trees), number of trees in the Lauraceae family/ha (category 1 and 2 trees), basal area (m^2/ha) (category 1 trees), tree species diversity (category 1 trees), elevation of each plot, and distance of each plot to a stream.

To determine general characteristics of the quetzal's cloud forest habitat which could affect quetzal distribution, the compositions of feeding resource tree species within categories 1 and 2 were separated into five groups for each category based on the similarity among plots of within plot tree species composition. Five species composition groups were chosen based on field observation of general forest types (Figure 1) and other site descriptions (Long & Heath 1991, Solórzano 1995). Tree species composition groups were determined using the Bray-Curtis dissimilarity index for the two categories. Significant differences between groups were determined using a PERMANOVA test. Analysis was done in R Studio version 1.2.5003. The spatial extents of these groups were determined based on the location of plots in each group and topographic features of the study area which could affect species composition (Breedlove 1981, Long & Heath 1991). Maps of these groups were created in QGIS version 3.14.

Significant differences between the species composition groups for the factors explaining quetzal abundance (fruit production or tree species composition characteristics) were tested using the Kruskal Wallis test in InfoStat. This was only done for the factors with significant correlations between quetzal abundance and within plot variables.

Results

Seasonal quetzal abundance patterns

Within the quetzals cloud forest reproductive habitat in El Triunfo, the average date of seasonal quetzal presence ranged from January 20 in 2011 to April 7 in 2012 (Figure 2, Table 1). Most years showed statistically significant seasonality of abundance, except 2010 (p=0.47) and 2018, although this was marginal (p=0.065). The year with the greatest seasonal concentration of quetzal abundance was 2012 (r=0.57). The mean dates of seasonal quetzal presence in 1992 (March 15) and 1993 (February 28) (Solórzano et al. 2000) were within the range of mean dates from years within 2010-2020, although the number of quetzal observations was much higher during the month of most observations in 1992-1993 compared to 2010-20 (Table 1).

Correlations between quetzal abundance, fruit production and rainfall

During the 17 months of fruit and quetzal observations between March 2019 and May 2021, there were significant correlations between quetzal abundance and the overall number of fruits estimated in the feeding resource tree community, the biomass of these fruits, and the number of tree species producing fruits (all $p<0.01$). Quetzal abundance was marginally correlated with the number of fruits estimated on species of the Lauraceae family ($p=0.08$), but not significantly correlated with the biomass of these fruits ($p=0.21$) (Table 2).

However, there were differences in significant correlations between quetzal observation periods when fruit production data was available (March 2019 – March 2020 and December 2020 – May 2021). Quetzal abundance was significantly correlated with the number of fruits produced by Lauraceae species between March 2019 and March 2020 ($p=0.022$), but not between December 2020 and May 2021 ($p=0.95$). In contrast to the overall significant correlations during the entire study period, quetzal abundance was only marginally correlated with overall community fruit number ($p=0.06$) and number of species producing fruits ($p=0.06$), and not significantly correlated with the biomass of fruit ($p=0.85$) during the second period (Table 2). From January 2013 to December 2020 quetzal abundance was significantly correlated (negatively) with monthly rainfall ($p<0.01$).

Spatial relations between quetzal abundance and habitat variables within the cloud forest

Local quetzal abundance (Figure 3) was spatially correlated with tree species diversity ($p=0.02$), and marginally with the number of Lauraceae species trees of all diameters ($p=0.06$). Quetzal abundance was also correlated (negatively) with elevation ($p<0.01$), and distance from streams ($p<0.01$), but not with mature trees/ha ($p=0.50$), mature Lauraceae tree/ha ($p=0.11$), all trees/ha (0.11), and basal area/ha (0.20). Between March 2019 and May 2021, overall local abundance of quetzals was significantly correlated with the biomass of Lauraceae fruit (p=0.05), marginally with the number of Lauraceae fruits (p=0.09), and not with the overall number of fruits (p=0.88) or biomass of fruits (p=0.55) (Table 3).

Distribution and composition of feeding resource species

The most common tree species were *Conostegia volcanalis*, *Eugenia capuli*, *Hedyosmum mexicanum* and *Symplococarpun purpusii*. The first three were mostly distributed in the wetter riparian areas, and the latter in the dryer slopes of the valley. These species also had the highest frequency among plots, due to their wide distribution in the study area. There were five species in the Lauraceae family within the plots. The most abundant of these species were *Nectandra rudis* and *Ocotea chiapensis*. Trees of these species were less abundant than others in the study area but had a larger overall basal area/ha than most species due to their large size. The other three Lauraceae species were some of the least common of the feeding resource trees (SM Table 2).

Spatial patterns of tree species compositions varied between Category 1 and 2 tree species groups. For Category 1, the five groups of species composition were found to represent: riparian (group 1), valley bottom and Pacific coastal slope (group 2), transition between the valley slopes and bottom (group 3), higher elevation crest of the mountain and an area of secondary forest (group 4), and valley slopes and secondary forest (group 5).

For category 2, the spatial distribution of the five groups of species composition was different in some aspects. There continued to be a group within the valley slopes and secondary forests (group 1). However, there were two groups within the higher elevations of the valley (group 2 and 4) and species composition within the valley bottom and riparian areas were grouped together (group 3). The valley slope-bottom transition was also similar in species composition for mature trees to the Pacific coastal side of the mountain (group 5) (Figure 4). All groups had significant differences in species compositions ($p<0.05$).

There were significant differences between category 1 species composition groups for number of Lauraceae trees/ha ($p=0.01$), species diversity ($p<0.01$), elevation of plots within each group ($p<0.01$), and distance of plots within each group to a stream ($p<0.01$); but not for quetzal abundance ($p=0.65$). Differences in quantity of Lauraceae fruit biomass between category 2 species composition groups were marginally significant ($p=0.07$) (Table 4).

Discussion

Seasonal abundance of quetzals in their cloud forest habitat

The abundance of quetzals in their cloud forest reproductive area was strongly seasonal during the 11 years of monitoring in El Triunfo, similarly to other observations throughout the distribution range of the quetzal in Mesoamerica (Bustamante et al. 2010, Powell & Bjork 1994, Solórzano et al. 2000). This seasonality appears to be strongly linked to the availability of fruits, although this relation was slightly different during 2019-2021 than 30 years earlier in El Triunfo.

In 1993, the average date of seasonal quetzal presence in the cloud forest (28 February) was much earlier in the year than that of the community fruit production (4 May) (Solórzano et al., 2000, Wootton et al. 2021), whereas it was very similar between fruit production and quetzal abundance in 1992 and 2019-2020. Between the early 1990's and 2019-2021, community fruit production patterns have shifted earlier in the year (Wootton et al. 2021b). However, seasonal quetzal abundance patterns were similar between 1992, 1993 and 2019. Differences in temporal relations between quetzal abundance and overall fruit availability could be due to differences in which species are producing fruits, slightly different areas of observation with differences in migration routes and tree species composition, or changes in forest composition and cover between 1991 and 2021 (Castro-Hernández 2019).

There was a significant correlation between availability of Lauraceae fruits and quetzal abundance within the first year of our study between March 2019 – March 2020, although not during December 2020 – May 2021. This contrasted with the findings of Solórzano et al. (2000) which did not find significant relations between quetzal abundance and production of Lauraceae fruits in El Triunfo during 1991-93, but our results were similar to those observed by Wheelwright (1983) in Costa Rica.

Some of the significant correlations during the first fruit observation period during 2019-20 were not significant during 2020-21. This could have been partially due to an extreme weather event between these periods. In November 2020, Hurricane Eta hit the Pacific coast of Mexico, and many trees and some trunks which had been used for the nests of quetzals fell in El Triunfo during this time. Fruit availability was also much lower in the months after the hurricane than during the same months in previous years (Wootton et al. 2021b), which coincided with a lower abundance of quetzals during its reproductive period in 2021 (December 2020 to May 2021) than in 2020.

The number of fruits in the Lauraceae family was also much lower in the six months after the hurricane than the same period the year before. This also may have been due to the effects of the hurricane, or a natural phenological behaviour of fruit production in some Lauraceae species with alternating years of high and low production, as was recorded by Wheelwright (1986) in Costa Rica. During the 2020-21 reproductive period, quetzals may have migrated to more sheltered areas less affected by the hurricane. A whole year of fruit availability observations in 2021 may also have shown stronger correlations during times of overall higher and lower quetzal and fruit presence in the cloud forest.

In addition to following fruit availability, other factors may explain the seasonality of quetzal abundance, since from 2013-2020, monthly quetzal abundance was negatively correlated with rainfall. Quetzals may be migrating to lower elevations in the Sierra Madre during the wet season when rainfall is greater at higher elevations, as was suggested as a reason for altitudinal migration by Boyle (2017). It may also be that the ability to detect quetzals is lower during the wet season because of the noise from heavy rainfall or reduced activity due to the rain. In addition to altitudinal migration, quetzals may migrate and be more locally abundant within certain parts of their cloud forest habitat due to fruit availability, tree species composition, and physical features of the landscape.

Spatial abundance of quetzals within the cloud forest

Although the altitudinal migration of the quetzal is now better known, the spatial relations with aspects of its cloud forest habitat have been less studied. We determined that the spatial abundance of quetzals within their reproductive habitat is related to the availability of Lauraceae fruit biomass, numbers of trees of the Lauraceae family and higher diversity of tree species. Lauraceae fruits are high in nutrients and an important part of the diet of newborn quetzals (Ávila et al. 1996, Carleton & Smith 2016). Adult quetzals require a higher density of fruit producing trees near to the nests to bring large quantities of fruits for their chicks (Carleton & Smith 2016). Given that different species produce fruit during different seasons of the year that coincide with the quetzal's reproduction, establishing a nest in an area with a higher diversity of fruit producing tree species may be essential for reproduction and chick survival.

There were differences between species composition groups in the number of Lauraceae species in category 1 (trees of all diameters), and marginally for Lauraceae fruit biomass in category 2 (mature trees with fruit producing potential). For category 1 species composition groups, there was a distinction between valley bottom and riparian areas, but not for category 2 trees. Lauraceae trees were more abundant in riparian areas followed by the valley bottom and transition areas, and less abundant in valley slopes and crests. However, some species such as *Nectandra rudis* and *Ocotea acuminatissima* grow throughout the study area so are more greatly represented within species groups when only mature tree diameters are considered. This may be a reason why quetzals were observed throughout the study area including the higher elevation valley crest areas.

Local quetzal abundance was also strongly correlated with diversity of tree species. The complexity of topography and environmental conditions in the study area has created conditions for a large diversity of species with changing species compositions throughout the valley. This diversity is important for the availability of feeding resources throughout the cloud forest and within a small area near to standing trunks which can be used by quetzals for their nests.

Within the category 1 species composition groups, the order of highest to lowest species diversity was: riparian, transition between the valley slopes and bottom, valley bottom, valley slope and crest areas (Table 4). Tree species diversity was also generally related to elevation and distance to streams, with higher diversity at lower elevations closer to streams. Other than species diversity differences, the environmental conditions of elevation and distance to streams may also be influencing quetzal abundance as the higher elevations are more exposed to stronger winds and rain, and the sheltered ravines often contain a higher abundance of rotten trunks suitable for nest sites and a water source for quetzals.

However, there was no significant difference in quetzal abundance between species composition groups. Therefore, it appears that quetzal abundance is related to tree species characteristics and fruit production in a smaller area (3 ha), rather than in a certain tree species composition group. As phenological fruit production patterns varied between species and years (Solórzano et al. 2000, Wootton et al. 2001b), the diversity of tree species between composition groups is important for the survival of quetzals throughout the year for both migrants and year-round resident individuals. This could explain the large variation in locations of quetzal observations throughout the year within the cloud forest.

Conservation implications

This study shows the importance of diversity of feeding resource tree species within the cloud forest reproductive habitat of the quetzal. The fruit species consumed by quetzals are also important feeding resources for other birds and mammals in the El Triunfo cloud forest (González-García et al. 2017, Lira-Torres et al. 2004). Monitoring of other animal species including tapir (*Tapirus bairdii*), spider monkey (*Ateles geoffroyi*), highland guan (*Penelopina nigra*) and horned guan (*Oreophasis derbianus*) which consume fruits and may migrate depending on the availability of these, has also been done since 2010. Ongoing monitoring of fruit production could help explain their movement and abundance patterns as well.

El Triunfo is an important example of how Mexican Biosphere Reserves are essential for the survival of threatened species such as the quetzal and its cloud forest habitats. Forest areas have been increasing since 1990 in the Sierra Madre (Wootton et al. 2021a). However, even within protected areas, threats from habitat alteration (e.g., loss of feeding resource trees near to nests; Renner 2005, Tejeda-Cruz & Sutherland 2005) and climate change (e.g., wildfire risk; Vilà-Vilardell et al. 2020) continue.

Since 1990, the wet season in the Sierra Madre has become wetter, but the end of the wet months has become dryer and months before the wet season begins are also dry (Wootton et al. 2021a). This has created conditions favouring the spread of wildfires, which burnt areas of quetzal habitat in April 2019. Our results show how tree species composition changes with local environmental conditions in topographically complex areas, and the importance of a high diversity of fruit producing tree species for quetzal abundance in the cloud forest. Restauration programs should include a high diversity of fruit producing tree species, and protection of streams and riparian forest cover in areas affected by deforestation and fires in El Triunfo and other areas of the quetzal's distribution. This will help to protect and increase the habitat of quetzals and other tropical mountain frugivores.

Acknowledgements

Monitoring of priority species in El Triunfo since 2010 was done by the park rangers and managers of the reserve, students as part of their social service, Mexican ecological researchers, and workers of environmental Civil Associations in Chiapas. We thank all these people for their contribution to this study; and the directors, managers and park rangers of the reserve for their help with field work and logistics: Juan Carlos Castro, Alexer Vázquez, Janette González, Rossana Megchun, Edilberto López, Abinaham López, Gilberto Argueta, Ramiro Gálvez, Ismael Gálvez, Adolfo Carbajal, Anelfo Gálvez, Joel Gómez, and Roberto Gálvez. Thanks to Marco Domínguez and Nathalia Castillo for help with the fieldwork, and Raúl Vazquez with the statistical analysis. Fieldwork and collection of fruits received permission form CONANP and SEMARNAT (No. SGPA/DGVS/8055/19). This project received funds from El Colegio de la Frontera Sur Department of Biodiversity Conservation, and the first author received a doctoral scholarship from CONACyT (No. 884660).

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Tables and Figures

Table 1. Seasonality of quetzal abundance in the cloud forest of polygon 1 of El Triunfo Biosphere Reserve, Chiapas, Mexico.

Year	Mean angle	Date	Vector r	Rayleigh z	Greatest abundance
1992	74±36	Mar 15	0.82	124 (<0.01)	March (80)
1993	59±60	Feb 28	0.57	47 (<0.01)	March (46)
2010	30±110	Jan 30	0.16	0.773 (0.47)	Apr/Oct (5)
2011	20±51	Jan 20	0.67	11.69 (<0.01)	February (6)
2012	97±61	Apr 7	0.57	20.41 (<0.01)	March (17)
2013	22±74	Jan 22	0.43	10.47 (<0.01)	February (11)
2014	54±55	Feb 23	0.63	19.00 (<0.01)	March (13)
2015	104±86	Apr 14	0.32	6.22 (0.002)	April (13)
2016	83±86	Mar 24	0.33	5.92 (0.003)	March (9)
2017	73±62	Mar 14	0.56	12.95 (<0.01)	February (10)
2018	89±99	Mar 30	0.23	2.73 (0.065)	Feb/Apr (8)
2019	59±63	Feb 28	0.54	23.98 (<0.01)	February (21)
2020	81±71	Mar 22	0.46	54.43 (<0.01)	February (22)

Table 2. Spearman correlation coefficients between monthly quetzal abundance, and fruit production and rainfall variables in the cloud forest of polygon 1 of El Triunfo, Chiapas, Mexico.

Variable	**2019-2021**	**2019-2020**	**2020-2021**
No. Fruits	0.84 (<0.001)	0.85 (<0.001)	0.83 (0.064)
Biomass	0.64 (0.006)	0.84 (0.001)	0.09 (0.848)
No. tree species	0.82 (<0.001)	0.87 (<0.001)	0.79 (0.059)
No. Lauraceae trees	0.43 (0.083)	0.68 (0.022)	-0.03 (0.949)
Biomass Lauraceae	0.32 (0.207)	0.41 (0.216)	-0.03 (0.949)
	2013-2020		
Monthly rainfall	-0.47 (<0.01)		

Table 3. Correlations between quetzal abundance at plot locations and fruit production, forest characteristics, and physical features of the reproductive habitat of the quetzal in the cloud forest of El Triunfo, Chiapas, Mexico.

Variable	**Coefficient**	**P-value**
3-year spatial-temporal relations (March 2019 – May 2021)		
No. ripe fruits	0.02	0.88
Biomass	0.08	0.55
No. Lauraceae fruits	0.24	0.09
Biomass Lauraceae fruits	0.27	**0.05**
11-year spatial relations (2010 - 2020)		
Trees/ha (mature)	0.10	0.48
Lauraceae trees/ha (mature)	0.20	0.16
Trees/ha (all)	0.22	0.12
Lauraceae trees/ha (all)	0.26	0.06
Basal area (m^2/ha)	0.16	0.26
Tree species diversity	0.29	**0.04**
Elevation	-0.43	**<0.01**
Distance to stream	-0.34	**0.01**

Table 4. Differences between species composition groups, in forest and physical characteristics and fruit production variables, using the Kruskal-Wallis H test. Variables are those where significant correlations with spatial quetzal abundance were determined. Group orders are from highest to lowest.

Variable	**H-value**	**P-value**	**Group order**
Category 1 groups (all trees)			
Lauraceae trees/ha	10.56	0.01	1,2,3,5,4
Tree species diversity	18.41	<0.01	1,3,2,5,4
Elevation	17.48	<0.01	5,4,3,2,1
Distance to stream	27.47	<0.01	3,4,5,2,1
Quetzal abundance	2.45	0.65	1,5,2,3,4
Category 2 groups (mature trees)			
Biomass Lauraceae fruits	7.39	0.07	3,5,2,1,4

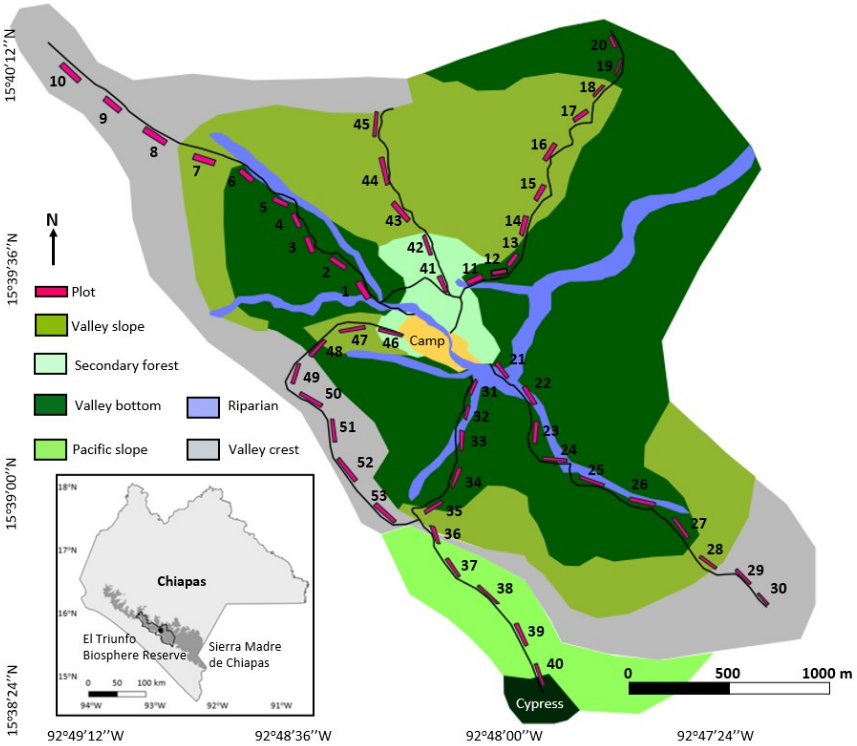

Figure 1. The study area in the central zone of polygon 1 of El Triunfo Biosphere Reserve, Chiapas, Mexico.

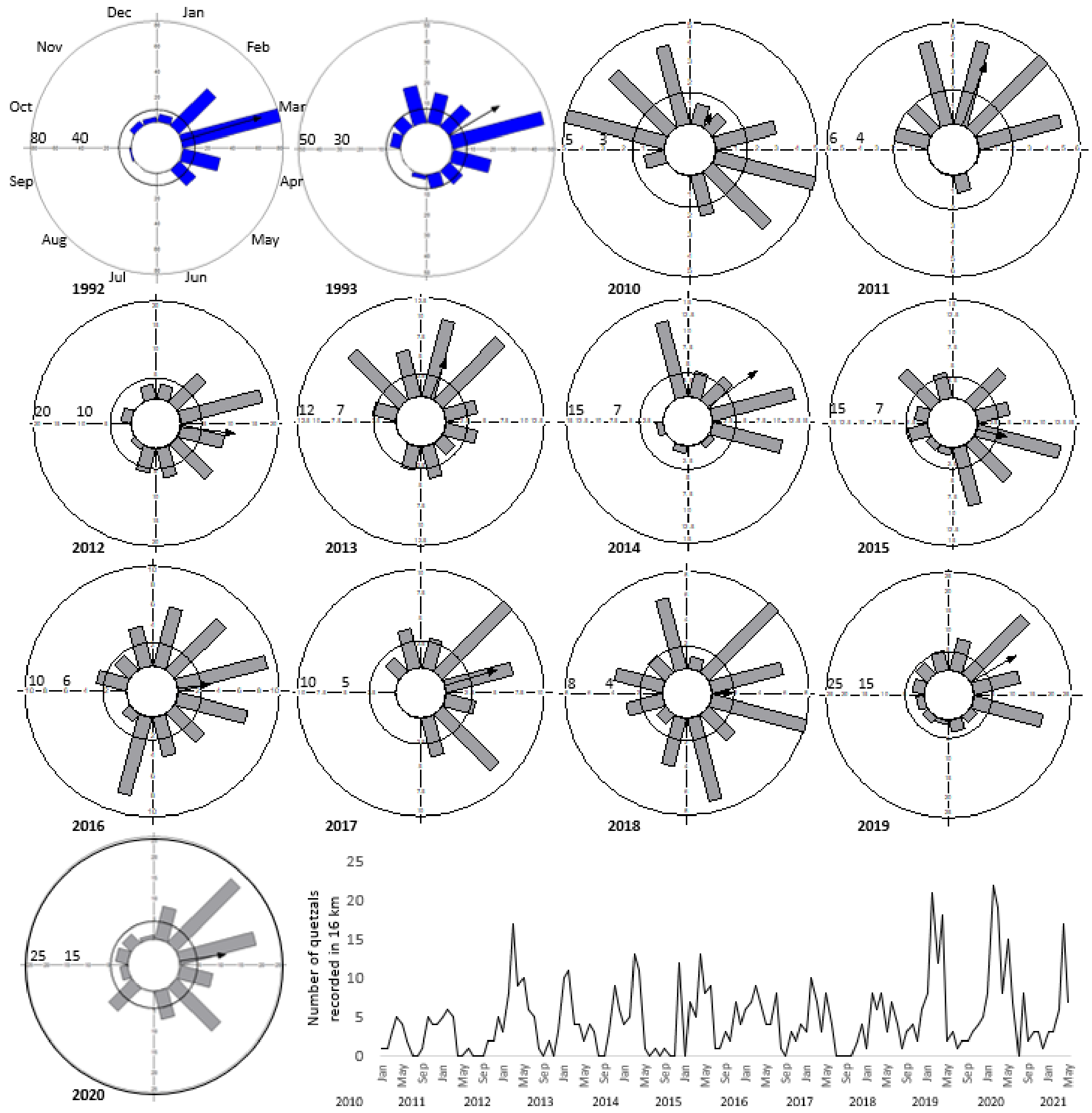

Figure 2. Circular histograms and graph of total number of quetzals observed monthly during 1992, 1993, and January 2010- May 2021 in the cloud forest of El Triunfo, Chiapas, Mexico.

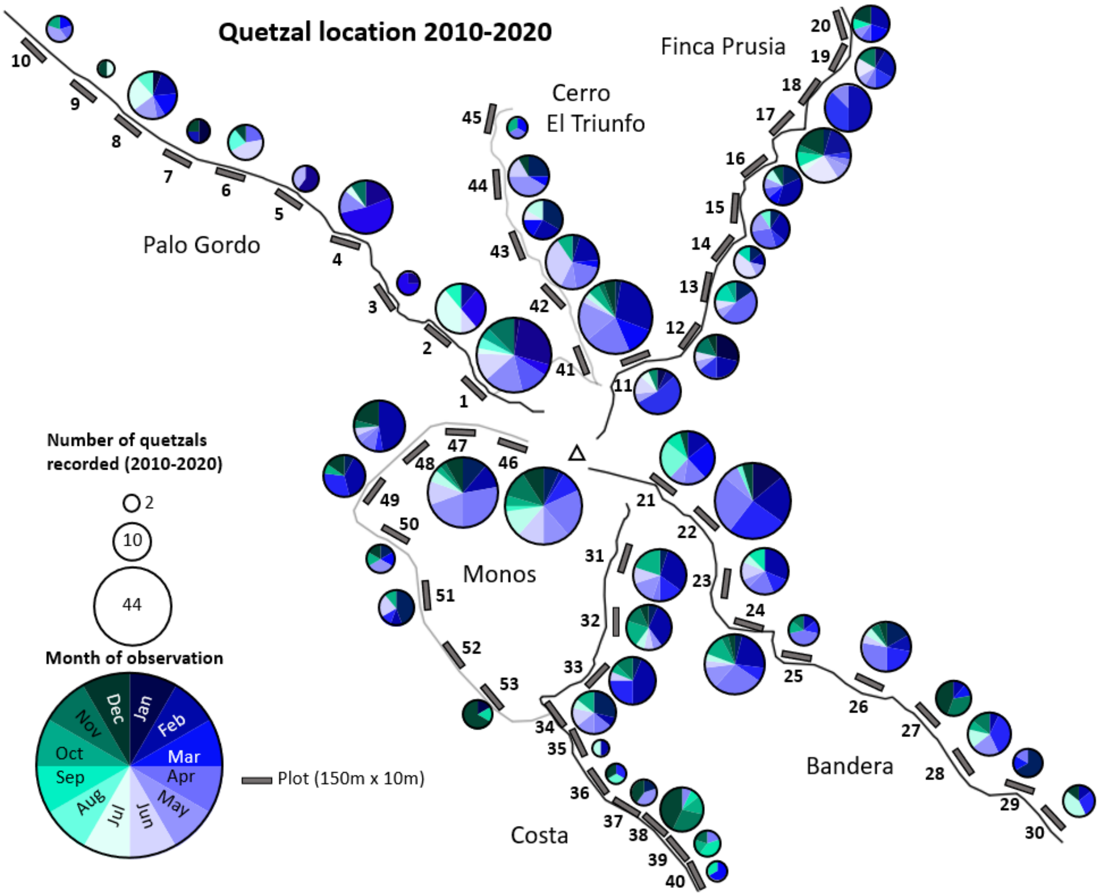

Figure 3. Month and total number of quetzal observations within 3 ha of a plot centre, between 2010 and 2020 in the central zone of polygon 1 of El Triunfo, Chiapas, Mexico.

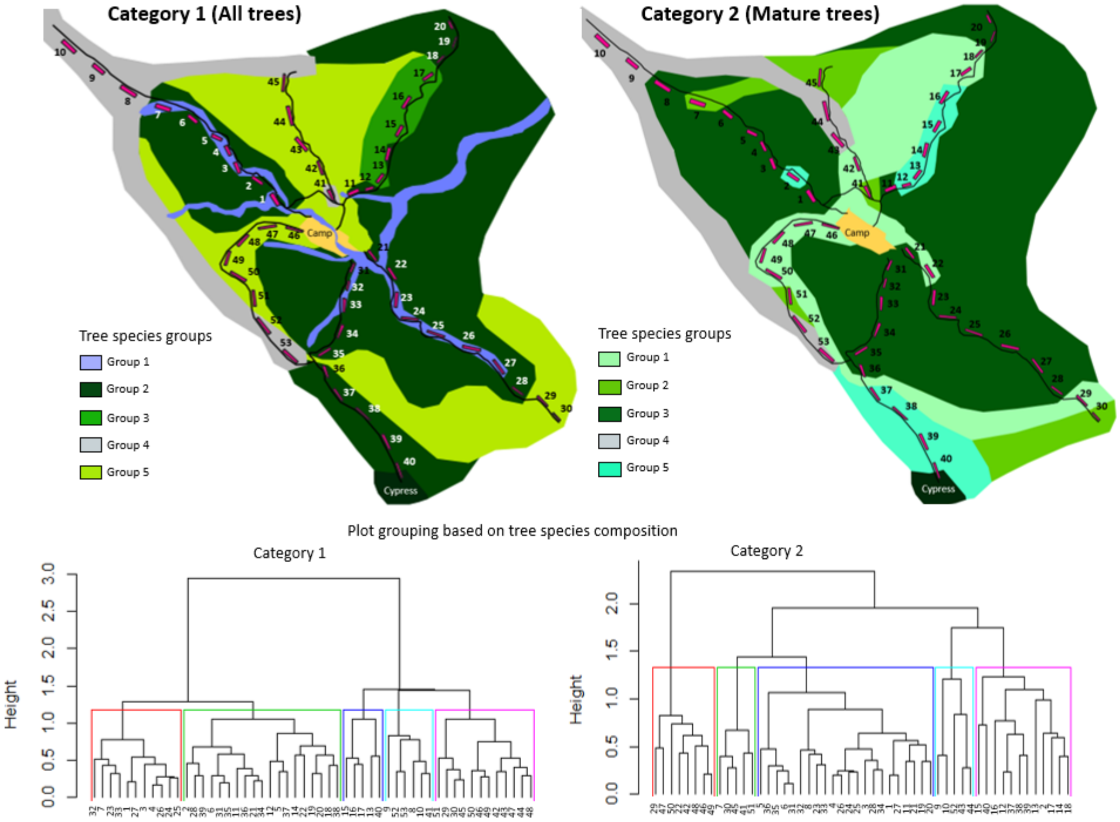

Figure 4. Cluster diagrams of the grouping of plots based on tree species compositions producing the feeding resources of the quetzal in Category 1 (all tree diameters), Category 2 (diameters of only mature fruit producing trees). Maps above the diagrams show the spatial distribution of the grouping of plots in the central zone of polygon 1 of El Triunfo, Chiapas, Mexico.

CAPÍTULO 5

Flores de *Ardisia compressa*. Foto de Allen Wootton.

CONCLUSIONES GENERALES

Los bosques nubosos de montaña son de los ecosistemas más amenazados en México debido a las presiones del uso del suelo y al cambio climático (Toledo-Aceves et al. 2011, Ponce-Reyes et al. 2012). Para aumentar su potencial de conservación, se ha recomendado que se incremente la protección de bosques de montaña en México dentro de las áreas protegidas (Ponce-Reyes et al. 2012, Rojas-Soto et al. 2012). Sin embargo, estas áreas todavía son susceptibles a los cambios de temperatura y lluvia impulsados por influencias regionales (Lawton et al. 2001, Barradas et al. 2010) y a gran escala (Pounds et al. 1999, Karmalkar et al. 2008). Los cambios climáticos están alterando los procesos ecológicos en los bosques nubosos en partes de Mesoamérica (Foster 2001, Neate-Clegg et al. 2018) y podrían cambiar las interacciones, comportamientos o distribuciones de varias especies (Şekercioğlu et al. 2012, Barnes 2015).

En este proyecto se determinó cómo algunos procesos ecológicos se relacionan con el clima y cambios en éste, en el bosque nuboso de la Reserva de la Biosfera El Triunfo, Chiapas. Para ello, el proyecto se centró en las relaciones entre las tendencias climáticas en la Sierra Madre, los patrones de floración y fructificación anuales y de largo plazo, y los patrones espaciales y temporales de abundancia de quetzal en la Reserva El Triunfo desde su establecimiento en 1990.

Cada una de las tres partes de este proyecto tuvo su propio objetivo general, con el fin de comprender mejor los procesos que influyen en los cambios e interacciones ecológicas en El Triunfo. El objetivo de la primera parte fue determinar si se han producido cambios en la temperatura y en las lluvias en la Sierra Madre, y cómo los factores regionales y de gran escala pueden haber influido en estos cambios. Encontramos que desde 1990, las temperaturas diarias mínimas han ido aumentado, mientras que las temperaturas diarias máximas han ido disminuyendo en la Sierra Madre. Casi todas las tendencias de la temperatura media diaria fueron más frías en la región, lo que contrasta con las tendencias más cálidas en la región costera adyacente localizada a menor elevación.

El rango decreciente de temperaturas diarias y tendencias frías durante los últimos ~30 años en la Sierra Madre corresponde a un periodo de tendencias crecientes de lluvia durante la temporada húmeda y tendencias más secas al final de ésta temporada. Los aumentos de lluvias en la temporada húmeda generalmente ocurrieron en todas las regiones de la Sierra Madre, la Depresión Central y la Costa de Chiapas, pero fueron mayores en la Sierra Madre que en las regiones de menor elevación. También hubo un desplazamiento general más temprano en el año al comienzo y al final de la temporada húmeda. Los aumentos en la cobertura de nubes asociados con el aumento de las lluvias podrían ser una explicación de la disminución del rango de temperatura diaria y las tendencias más frías, ya que las nubes bloquean la radiación solar entrante durante el día y reflejan la radiación de onda larga saliente durante la noche.

Estas tendencias en la temperatura y las lluvias ocurrieron durante una época de incremento en las temperaturas de la superficie del mar en el Mar Caribe y el Golfo de México (Lluch-Cota et al. 2013), un cambio de la fase positiva a la negativa de la Oscilación Decadal del Pacífico (NOAA 2020b) y aumentos del CO_2 atmosférico (NOAA 2020a). Estas condiciones cambiantes a gran escala se han asociado con las características de las tendencias climáticas determinadas para las regiones del Pacífico de Chiapas (Liverman y O'Brien 1991, Aguilar et al. 2005, Méndez-González et al. 2010). Además, los incrementos regionales en la densidad de la cobertura vegetal desde 1990 pueden haber aumentado los efectos de las influencias a gran escala en las tendencias climáticas regionales, a través del reciclaje de la humedad de origen oceánico a partir de la evapotranspiración de la vegetación regional (Durán -Quesada et al. 2012, Sheil 2018).

Los efectos de estas tendencias climáticas en los patrones de floración y fructificación en el bosque nuboso de El Triunfo, fue el foco del objetivo de la segunda parte del proyecto. Esto fue para determinar las relaciones entre las variables climáticas (temperatura, lluvia mensual, duración del día y radiación solar) y patrones fenológicos en especies arbóreas del bosque nuboso de El

Triunfo, y si estos patrones han cambiado después de ~30 años. Existieron correlaciones significativas y negativas entre floración y temperatura, duración del día y lluvia; y fructificación inmadura y temperatura, duración del día y radiación solar. También hubo correlaciones significativas y positivas entre la fructificación madura y la radiación solar para la intensidad y el número de frutos, pero no hubo correlación significativa para la biomasa de frutos.

Se registró un cambio general más temprano en el año en los patrones fenológicos de la comunidad de árboles entre 2019-21 y 1992-93. La fecha media de producción de frutos estacional en 2019-20 fue el 12 de marzo, mientras que en 1992 fue el 29 de marzo y en 1993 fue el 4 de mayo. El desplazamiento más temprano en el año en el comienzo de la temporada húmeda y los aumentos en las lluvias durante ésta temporada pueden haber influido en el cambio fenológico, como se observó en otros bosques tropicales con tendencias climáticas similares (Dunham et al. 2018). Un posible aumento en la cobertura de nubes asociado con el aumento de las lluvias a principios de año podría haber bloqueado parte de la radiación solar entrante y acortado los tiempos de maduración de los frutos durante marzo y abril. También un posible aumento en la presencia de frugívoros en el momento de la maduración podría haber aumentado la aparente estacionalidad y el cambio más temprano de los patrones de presencia de los frutos maduros.

El plan original para este estudio fue obtener observaciones fenológicas continuas durante dos años (2019 y 2020). Sin embargo, después de marzo de 2020, la pandemia de Covid-19 y las restricciones de viaje locales requirieron que las observaciones se pospusieran hasta diciembre de 2020 y se extendieran hasta mayo de 2021. Durante este periodo, el huracán Eta golpeó la costa del Pacífico de Chiapas en noviembre de 2020 y muchos árboles en El Triunfo cayeron como resultado, incluidos algunos de los árboles etiquetados para observación en este estudio. Esto suceso estocástico nos brindó la oportunidad de estudiar no solo los efectos de las tendencias climáticas a largo plazo en los patrones fenológicos, sino también los efectos de este huracán (Eta) en la presencia de frutos entre años. Las comparaciones de los mismos periodos de seis meses antes y después del huracán encontraron que la fecha estacional promedio de presencia de frutos de la comunidad arbórea fue dos semanas más tarde en el año posterior al huracán, con una mayor estacionalidad (un periodo más estrecho de la presencia de frutos) y una disminución significativa en el número de frutos, en comparación con los mismos meses durante 2019-20. Predijimos que estos cambios en los patrones de fructificación tuvieran un efecto en los patrones de abundancia del quetzal en esta área, que es un hábitat de reproducción importante para esta especie.

Esta información fenológica, así como las mediciones de la composición de árboles en 53 parcelas, se utilizaron como base para el objetivo final del proyecto. Esto fue para determinar los patrones de abundancia anual del quetzal en su hábitat reproductivo del bosque nuboso de El Triunfo, y si estos patrones estaban relacionados espacial y temporalmente con la abundancia de los frutos y las características de la composición de las especies arbóreas. Entre 2010 y 2020, la fecha promedio de presencia del quetzal osciló entre enero y abril en el bosque nuboso de El Triunfo. Desde 2019-21 hubo correlaciones significativas entre la abundancia mensual general de quetzales y (1) el número mensual de frutos en la comunidad de recursos alimentarios, (2) la biomasa de estos frutos, (3) el número de especies con frutos y marginalmente con el número de frutos de Lauraceae. La abundancia del quetzal también se correlacionó negativamente con la lluvia mensual durante el periodo entre enero de 2013 y diciembre de 2020.

Hubo correlaciones espaciales entre la abundancia local de la población del quetzal (en 3 ha alrededor del centro de cada parcela) y la diversidad de especies arbóreas, el número de árboles de Lauraceae/ha (marginalmente), la biomasa de frutos de Lauraceae y la cercanía a los arroyos. La composición de especies arbóreas varió mucho a lo largo del valle de la zona núcleo del polígono 1, con cinco grupos generales de composición de especies arbóreas distribuidos en áreas con diferentes condiciones físicas o topográficas. La composición del bosque (mayor diversidad de especies de árboles y numero de árboles de la familia Lauraceae) y las características de producción de frutos (mayor biomasa de frutos de Lauraceae) que se correlacionaron significativamente con la abundancia de quetzal, fueron generalmente mayores en las áreas riparias, seguidas por el fondo del valle y la pendiente de la costa del Pacífico, un área de transición entre las laderas del valle y el fondo del valle, las laderas del valle y el bosque secundario, y fueron menores en las áreas de cresta más elevadas y expuestas al viento.

Los resultados de esta tesis muestran cómo la complejidad de los comportamientos fenológicos en respuesta a los cambios estaciónales de las variables climáticas en una comunidad arbórea diversa, y en un paisaje heterogéneo, crea condiciones de asincronía espacial y temporal de los recursos alimentarios para los quetzales y otros frugívoros. Estas condiciones favorecen la abundancia y conservación de los quetzales en su hábitat reproductivo de mayor elevación de El Triunfo, y otras áreas de la Sierra Madre.

Algunos factores que influyen en el clima de El Triunfo, como el aumento del CO_2 atmosférico, pueden estar provocando cambios a largo plazo en los patrones de temperatura y lluvia en esta región (Karmalkar et al. 2008, Ponce-Reyes et al. 2012). Otros factores son cíclicos durante un periodo de 30 años o más (Méndez-González et al. 2010, Fuentes-Franco et al. 2015). Por lo tanto, los patrones fenológicos en El Triunfo pueden cambiar durante los próximos 30 años en comparación con los cambios en los patrones de los últimos 30 años. Los patrones del ciclo de fructificación anual y las relaciones espacio-temporales con la abundancia del quetzal pueden variar debido a factores bióticos, cambios anuales en la temperatura y las lluvias y eventos climáticos extremos, y desplazamientos en la fructificación por los cambios en las tendencias climáticas a futuro.

Implicaciones para la conservación

Este proyecto se enfocó en la fenología de los frutos y la composición de las especies de árboles con relación a la abundancia del quetzal. Esto puede proporcionar información útil para ayudar a explicar las razones del cambio en el patrón de abundancia y los requisitos de hábitat del quetzal en un bosque nuboso. El monitoreo que se realiza de especies prioritarias en la Reserva de la Biosfera El Triunfo desde 2010, también ha incluido otras cuatro especies de frugívoros: pavón (*Oreophasis derbianus*), pajuil (*Penelopina nigra*), tapir (*Tapirus bairdii*) y mono araña (*Ateles geoffroyi*) (CONANP 2020). Entonces, una implicación importante es que se podrían realizar análisis similares utilizando los datos de observaciones de estas especies con los datos ahora disponibles de la producción de frutos y la composición de especies de árboles obtenidos en este proyecto, para ayudar a comprender sus patrones de abundancia y necesidades de hábitat.

Los resultados del capítulo 4 muestran que, al considerar las especies productoras de frutos consumidos por los quetzales, la composición de especies locales es muy diversa dentro de esta área de bosque nuboso. Los resultados también sugieren que esta diversidad es un componente muy importante para el hábitat del quetzal y proporciona complementariedad del hábitat (Dunning et al. 1992, Powell et al. 2000) a través de la producción de frutos de las especies en diferentes épocas del año. Esta comprensión de la composición de las especies de árboles y su relación con las características físicas de este paisaje montañoso (laderas de los valles, fondos de los valles, áreas riparias y crestas) puede ser útil como referencia de la variabilidad de hábitat necesaria para la restauración ecológica del hábitat del quetzal en las tierras altas de montaña con áreas agrícolas abandonadas o quemadas de la Sierra Madre. Las áreas quemadas dentro del hábitat del quetzal, como las que ocurrieron después de los incendios forestales en abril de 2019, pueden ser más comunes en el futuro si continúan las tendencias en la reducción progresiva de la humedad en la estación seca.

Por ello, se recomienda que los programas de restauración incluyan una alta diversidad de especies arbóreas que producen frutos y están presentes en el área local. La protección y restauración de arroyos, cañadas y áreas riparias también serán necesarios para mantener los hábitats críticos. Estas acciones serán importantes para proteger y aumentar el hábitat de quetzales y otras especies frugívoras en El Triunfo.

Recomendaciones para estudios futuros

Este estudio se llevó a cabo en la zona núcleo del polígono 1 El Triunfo. Esto con la finalidad de comparar las observaciones de los patrones fenológicos de frutos de 2019-2021 con las observaciones realizadas en 1991-1993, y también incorporar los datos de abundancia del quetzal del monitoreo de especies prioritarias de 2010-2020 de la reserva. Sin embargo, como muchas de las especies frugívoras, incluido el quetzal, migran altitudinalmente o hacia otras partes del bosque nuboso durante el año, los estudios fenológicos en otras elevaciones y tipos de bosques podrían ser útiles para ayudar a explicar sus patrones de movimiento.

Estos estudios podrían incluir el tramo del sendero Costa entre El Limonar y Caña Honda en el lado costero, y entre el antiguo campamento de Palo Gordo y el borde de los cafetales de Finca Catarina. Las comparaciones fenológicas de la producción de frutos también se podrían hacer con otros hábitats de bosques nubosos como los del polígono 2 (Ovando) o el polígono 3 (Quetzal). En el polígono 1, se ha observado que los quetzales consumen los frutos carnosos de la mayoría de las especies de árboles que los producen. Por lo tanto, los estudios en otras áreas podrían incluir todas las especies observadas en este estudio, así como las especies locales que producen frutos carnosos.

Tanto los periodos de observación fenológicos de 1991-1993 (Solórzano 1995) como los de 2019-2021 (Capítulo 3) estuvieron limitados por la duración de estos estudios. Las observaciones fenológicas adicionales o continuas en la misma área también podrían ser útiles para determinar la variación de un año a otro en la producción de flores y frutos, y ayudar a explicar los patrones de abundancia de las especies frugívoras incluidas en el programa de monitoreo.

Como se mencionó para las implicaciones de conservación del proyecto, además de los quetzales, el monitoreo de especies desde 2010 ha incluido otras cuatro especies de frugívoros. Los datos de ubicación y abundancia de estas especies, u otras como el tucán esmeralda (*Aulacorynchus prasinus*), también podrían estar relacionados con la producción de frutos y los datos de especies arbóreas de las 53 parcelas dentro del área de estudio, como sucedió con los quetzales en este estudio. Se recomienda seguir con el monitoreo biológico, pero también es importante considerar factores ecológicos, como la disponibilidad de alimentos y la estructura y composición de árboles en los hábitats, para ayudar a explicar las variaciones en las abundancias de los animales.

Durante el segundo año del doctorado, se había planeado incluir dentro del proyecto un análisis de los nutrientes en los frutos. Sin embargo, debido a la pandemia y al cierre de laboratorios, no fue posible realizar este análisis. Los estudios futuros de los nutrientes de los frutos (contenido de agua, lípidos, minerales, carbohidratos y proteínas) de las especies consideradas en este estudio podrían proporcionar información útil para las relaciones espacio-temporales frugívoro/fruto, además de los datos fenológicos y de composición de especies arbóreas. Asimismo, podrían ser útiles para planificar la dieta de especies en cautiverio como en el ZooMAT en Tuxtla Gutiérrez, Chiapas.

Finalmente, los resultados de este proyecto sugieren que las tendencias de temperatura y lluvia han afectado los procesos ecológicos y las interacciones en los bosques nubosos de la Reserva de la Biosfera El Triunfo. Esta es solo una parte de una de las cuatro Reservas de la Biosfera (El Triunfo, La Sepultura, Volcán Tacaná y La Encrucijada) en la Sierra Madre y costa de Chiapas. Como se muestra en el Capítulo 2, las lluvias han aumentado considerablemente en las mayores elevaciones de la Sierra Madre desde 1990 y esto podría haber afectado las condiciones ambientales en las menores elevaciones a través del aumento de los caudales de los ríos que afectan los niveles de agua de los humedales, los nutrientes y la salinidad costera en los manglares.

También se han producido tendencias significativas de temperatura y lluvias regionales o locales desde 1990 en otras partes de la región Pacífico de Chiapas donde se encuentran estas Reservas de la Biosfera, y se ha realizado el monitoreo de otras especies (SEMAHN 2021). En estas áreas también se podrían realizar estudios comparativos y de relaciones entre el clima y las tendencias y patrones ecológicos, similares a este proyecto. El intercambio de esta información entre reservas podría ser útil para comprender las relaciones climáticas y ecológicas regionales interconectadas en la costa y las montañas costeras de Chiapas.

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ANEXOS

MATERIAL SUPLEMENTARIO

CAPÍTULO 2. Regional patterns of vegetation, temperature, and rainfall trends in the coastal mountain range of Chiapas, Mexico

SM Table I. Coordinates and elevations of the weather stations with data used for the analysis of temperature (indicated with T), potential evapotranspiration (PET) and monthly rainfall (R).

Weather Station	Analysis variable	Latitude	Longitude	Elevation (m.a.s.l.)	Region
Adolfo Ruiz Cortínez	T/PET	14.875000	-92.537500	4	Coast
Arriaga	T/PET/R	16.241667	-93.908333	64	Coast
Cacahoatan	R	14.988333	-92.164444	480	Coast
Cacaluta	T/PET/R	15.365	-92.731111	80	Coast
Chahuites	T/PET/R	16.25	-94.233056	23	Coast
Despoblado	T/PET/R	15.2025	-92.558056	63	Coast
Ejido Ibarra	R	15.333889	-92.952222	9	Coast
El Dorado	T/PET/R	14.672778	-92.212778	35	Coast
Escuintla (DGE)	T/PET/R	15.330833	-92.655833	92	Coast
Finca Argovia	R	15.126667	-92.299167	620	Coast
Francisco Sarabia	T/PET/R	15.417778	-92.998333	25	Coast
Frontera Hidalgo	T/PET/R	14.777222	-92.176111	60	Coast
Horcones	T/PET	15.955278	-93.605556	130	Coast
Huehuetán	T/R	15.002222	-92.400278	65	Coast
Independencia	T/PET/R	15.348333	-92.578333	112	Coast
Ingacio Lopez Rayón	T/PET/R	14.617778	-92.184722	7	Coast
Las Brisas	T/PET/R	15.514444	-93.116944	10	Coast
Mazatán	T/PET/R	14.886389	-92.453889	15	Coast
Medio Monte	T/PET/R	14.915278	-92.190556	245	Coast
Metapa de Domínguez	R	14.831111	-92.191667	98	Coast
Pijijiapan	T/PET/R	15.697778	-93.211389	57	Coast
Plan de Iguala	T/PET/R	14.958889	-92.504167	18	Coast
Salvación	T/PET/R	15.143889	-92.701389	8	Coast
San Isidro	R	15.742778	-93.351389	45	Coast
San Jerónimo	T/R	15.039722	-92.136389	750	Coast
Santo Domingo	T/R	15.0275	-92.104167	859	Coast
Talismán I	R	14.963056	-92.147222	340	Coast
Tapachula	T/PET/R	14.920833	-92.25	193	Coast
Tonalá	T/PET/R	16.084167	-93.743889	55	Coast
Tres Picos	T/PET/R	15.875	-93.545833	20	Coast
Buenos Aires	T/PET/R	15.3325	-92.2675	1820	Sierra Madre
El Porvenir	T/PET/R	15.457222	-92.281111	2847	Sierra Madre
Finca A. Prusia	R	15.731944	-92.794167	1040	Sierra Madre
Finca Chicharras	T/PET/R	15.133056	-92.242222	1328	Sierra Madre
Finca Cuxtepeques	T/PET/R	15.728611	-92.968889	1550	Sierra Madre
Finca Germania	R	15.194444	-92.345833	1214	Sierra Madre
Finca Hamburgo	R	15.173089	-92.325278	1200	Sierra Madre
Frontera Amatenango	T/PET/R	15.433611	-92.114167	900	Sierra Madre
Monterrey	PET/R	16.058889	-93.368889	700	Sierra Madre

Motozintla	T/R	15.364167	-92.248056	1260	Sierra Madre
Reforma II	T/PET/R	15.9	-92.933333	700	Sierra Madre
Unión Juárez	T/PET/R	15.0625	-92.080556	1300	Sierra Madre
Úrsulo Galván	T/PET/R	16.278611	-93.418611	700	Sierra Madre
El Triunfo	PET	15.6566	-92.8081	1973	Sierra Madre
Sierra Madre 1	PET	15.5497	-92.6268	1898	Sierra Madre
Sierra Madre 2	PET	15.8709	-93.1338	1896	Sierra Madre
Sierra Madre 3	PET	16.1977	-93.6121	2366	Sierra Madre
Acala	T/PET/R	16.552778	-92.804167	420	Central Depression
Aquespala	R	15.794167	-91.920278	617	Central Depression
Benito Juárez	R	16.082778	-92.840556	580	Central Depression
Berriozabal	T/R	16.796944	-93.265278	890	Central Depression
Cascajal	T/PET/R	16.308889	-92.486111	650	Central Depression
Catarinitas	T/PET/R	15.9025	-92.482778	945	Central Depression
Chicomuselo	T/PET/R	15.751667	-92.273611	550	Central Depression
El Boquerón	T/PET/R	16.644167	-93.157222	500	Central Depression
El Progreso	T/R	16.708889	-93.4025	781	Central Depression
Finca Ocotlán	T/PET/R	16.369444	-93.477222	650	Central Depression
Flores Magón	R	16.393333	-92.696111	482	Central Depression
Francisco I. Madero	R	16.802778	-93.755278	736	Central Depression
Guadalupe Grijalva	T/PET/R	15.693611	-92.161111	630	Central Depression
Jaltenango	T/PET/R	15.870833	-92.723889	640	Central Depression
La Angostura (CFE)	T/R	16.419722	-92.767778	500	Central Depression
La Mesilla	T/R	16.184167	-92.2875	1210	Central Depression
La Unión	T/PET/R	16.665	-93.800833	580	Central Depression
Las Flores	T/R	16.691944	-93.563056	480	Central Depression
Ocozocoautla	R	16.750883	-93.373889	838	Central Depression
Paso Hondo	R	15.684444	-92.006944	660	Central Depression
Portaceli	PET/R	16.449167	-93.125278	780	Central Depression
Puente Colgante	T/PET/R	16.740556	-93.031111	418	Central Depression
Puente Concordia (CFE)	T/PET/R	15.848611	-91.968056	582	Central Depression
Querétaro	R	15.838611	-92.755556	665	Central Depression
Revolucion Mexicana	T/PET/R	16.163056	-93.076389	540	Central Depression
Rosendo Salazar	R	16.471111	-94.003889	721	Central Depression
San Miguel	T/PET/R	15.708611	-92.208611	600	Central Depression
Soyatitán	T/PET/R	16.288889	-92.428333	832	Central Depression
Tuxtla Gutierrez (CFE)	T/PET/R	16.761667	-93.102778	532	Central Depression
Villa Corso	R	16.194444	-93.2625	600	Central Depression
Villa de Chiapilla	R	16.5775	-92.715278	550	Central Depression
Villaflores	T/PET/R	16.228889	-93.2625	554	Central Depression
Abelardo L. Rodríguez	R	16.379167	-92.2375	1920	Central Highlands
La Cabaña	R	16.714167	-92.628889	2113	Central Highlands
La Trinitaria (CFE)	T/PET/R	16.117778	-92.051667	1540	Central Highlands

SM Table II. Landsat satellite images used for classification of vegetation types and estimation of evapotranspiration.

Path	**Row**	**Season**	**Date**	**Landsat**	**Bands Used for Classification**	**Bands Used for NDVI**
1990 (1987-1992)						
22	49	Transition	19 December 1987	5	2,3,4	3,4
21	49	Transition	3 February 1990	5	2,3,4	3,4
21	50	Transition	1 December 1989	5	2,3,4	3,4
22	49	Dry	19 March 1992	5	2,3,4	3,4
21	49	Dry	19 April 1991	5	2,3,4	3,4
21	50	Dry	19 April 1991	5	2,3,4	3,4
22	49	Wet	19 November 1988	5	2,3,4	3,4
21	49	Wet	14 August 1987	5	2,3,4	3,4
21	50	Wet	8 July 1991	5	2,3,4	3,4
2005 (1997-2011)						
22	49	Transition	22 December 1997	5	2,3,4	3,4
21	49	Transition	1 February 1998	5	2,3,4	3,4
21	50	Transition	16 November 1998	5	2,3,4	3,4
22	49	Dry	1 April 2011	5	2,3,4	3,4
21	49	Dry	9 April 1999	5	2,3,4	3,4
21	50	Dry	8 March 1999	5	2,3,4	3,4
22	49	Wet	24 August 2000	5	2,3,4	3,4
21	49	Wet	16 July 2000	5	2,3,4	3,4
21	50	Wet	24 July 1997	5	2,3,4	3,4
2020 (2017-2020)						
22	49	Transition	11 January 2017	8	3,4,5	4,5
21	49	Transition	28 December 2019	8	3,4,5	4,5
21	50	Transition	28 December 2019	8	3,4,5	4,5
22	49	Dry	23 April 2019	8	3,4,5	4,5
21	49	Dry	26 April 2017	8	3,4,5	4,5
21	49	Dry	29 January 2020	8	3,4,5	4,5
21	50	Dry	11 February 2019	8	3,4,5	4,5
22	49	Wet	29 August 2019	8	3,4,5	4,5
21	49	Wet	5 July 2019	8	3,4,5	4,5
21	50	Wet	16 August 2017	8	3,4,5	4,5

SM Table III. Comparison of Potential Evapotranspiration (PET) methods for seven weather stations located within or near to the study area for days representing the dry (1 May 2020), and wet (25 July 2020) seasons. Percent Errors between each of the simpler PET methods used in comparison with the Penman Monteith (PM) method are shown between parenthesis.

Weather Station	**Season**	Potential Evapotranspiration value (mm/day) **PM**	**Thornthwaite**	**Hargreaves**	**Turc**
COAST					
Tapachula	Dry	5.44	5.45 (0.2)	5.98 (9.9)	5.04 (-7.4)
	Wet	4.79	5.30 (10.6)	5.96 (24.4)	5.10 (6.4)
Escuintla	Dry	4.34	5.07 (16.9)	6.42 (48.0)	5.52 (27.3)
	Wet	4.73	5.04 (6.6)	5.80 (22.7)	5.06 (7.0)
SIERRA MADRE					
El Triunfo	Dry	4.35	4.09 (-5.9)	4.19 (-3.7)	3.92 (-9.8)
	Wet	3.83	4.13 (7.8)	3.45 (-9.8)	3.29 (-13.9)
Volcán	Dry	2.91	4.29 (47.4)	4.36 (50.0)	4.06 (39.7)
Tacaná	Wet	1.36	4.19 (208.5)	3.35 (146.6)	3.21 (136.6)
CENTRAL DEPRESSION/HIGHLANDS					
Comitán	Dry	4.98	4.60 (-7.6)	4.55 (-8.6)	4.16 (-16.5)
	Wet	4.74	4.72 (-0.5)	4.78 (0.7)	4.33 (-8.7)
Tuxtla	Dry	5.28	4.92 (-6.7)	5.08 (-3.7)	4.51 (-14.5)
	Wet	4.90	4.99 (1.9)	5.65 (15.3)	4.96 (1.3)
Lagunas de	Dry	2.32	4.24 (82.5)	3.58 (54.1)	3.41 (46.7)
Montebello	Wet	3.34	4.42 (32.3)	4.72 (41.4)	4.35 (30.5)

SM Table IV. Changes in average daily temperature between 1990 and 2016 in the Central Depression (CD), Sierra Madre, and Coast regions of Chiapas, Mexico. Only weather stations with significant ($p<0.05$) temperature trends are included. Significant temperature trends during the longer 1960-2016 period at the same stations are indicated in the far-right column (Trend since 1960), where data are available since 1960. Details of these trends are shown in SM table VI.

Area	**Weather Station**	**Season**	**No. of data**	**Regression value**	**P-value**	**Change (ºC)**	**Trend**	**Trend since 1960**
CD	Catarinitas	Dry-cool	24	0.2336	0.018	2.7	Warm	
CD	Guadalupe Grijalva	Dry-cool	25	0.2009	0.047	-1.4	Cool	Yes
CD	Jaltenango	Dry-cool	27	0.3876	0.000	-1.1	Cool	
CD	Soyatitán	Dry-cool	27	0.646	<0.0001	-3.5	Cool	
CD	La Mesilla	Dry-cool	27	0.7258	0.05	-5.0	Cool	
CD	Tuxtla Gutierrez (CFE)	Dry-cool	26	0.6112	<0.0001	-2.9	Cool	
CD	El Progreso	Dry-cool	27	0.558	<0.0001	2.0	Warm	Yes
CD	Catarinitas	Dry-hot	24	0.6103	0.001	6.0	Warm	
CD	Guadalupe Grijalva	Dry-hot	25	0.2772	0.003	2.5	Warm	No
CD	Jaltenango	Dry-hot	27	0.2017	0.033	-1.0	Cool	
CD	Soyatitán	Dry-hot	27	0.318	<0.0001	-1.5	Cool	
CD	La Mesilla	Dry-hot	27	0.4293	0.000	-3.1	Cool	
CD	Tuxtla Gutierrez (CFE)	Dry-hot	26	0.3435	0.005	-2.2	Cool	
CD	El Progreso	Dry-hot	27	0.5245	<0.0001	2.5	Warm	No
CD	Catarinitas	Wet	24	0.5763	0.002	5.2	Warm	
CD	Guadalupe Grijalva	Wet	25	0.2547	0.023	3.1	Warm	No
CD	Jaltenango	Wet	27	0.3518	0.001	-1.4	Cool	
CD	Soyatitán	Wet	27	0.2293	<0.0001	-1.2	Cool	
CD	La Mesilla	Wet	27	0.28	0.009	-2.3	Cool	
CD	Tuxtla Gutiérrez (CFE)	Wet	26	0.3517	0.009	-1.8	Cool	
CD	El Progreso	Wet	27	0.6608	<0.0001	3.3	Warm	No
Sierra	Buenos Aires	Dry-cool	27	0.3447	0.003	-1.8	Cool	
Sierra	Frontera Amatenango	Dry-cool	26	0.4652	0.000	-3.5	Cool	No
Sierra	Motozintla	Dry-cool	26	0.3686	0.011	-1.9	Cool	No
Sierra	Ursulo Galvan	Dry-cool	23	0.3038	0.023	-1.8	Cool	
Sierra	Buenos Aires	Dry-hot	27	0.236	0.010	-0.9	Cool	
Sierra	Reforma II	Dry-hot	27	0.3049	0.008	1.2	Warm	
Sierra	Motozintla	Dry-hot	26	0.2678	0.025	-2.0	Cool	No
Sierra	Ursulo Galván	Dry-hot	23	0.2135	0.039	-1.3	Cool	
Sierra	Buenos Aires	Wet	27	0.108	0.023	-1.0	Cool	
Sierra	Ursulo Galván	Wet	23	0.5223	0.001	-2.2	Cool	
Coast	Pijijiapan	Dry-cool	27	0.2785	0.010	0.9	Warm	Yes
Coast	Tapachula	Dry-cool	27	0.878	<0.0001	2.5	Warm	Yes
Coast	Escuintla	Dry-cool	27	0.6687	<0.0001	2.8	Warm	Yes
Coast	Plan de Iguala	Dry-cool	26	0.1355	0.029	0.9	Warm	
Coast	Huehuetán	Dry-cool	27	0.5034	0.021	1.3	Warm	
Coast	Salvación	Dry-cool	27	0.5077	0.000	2.7	Warm	
Coast	Ignacio Lopez Rayón	Dry-cool	26	0.5177	0.000	-1.8	Cool	Yes
Coast	Pijijiapan	Dry-hot	27	0.1376	0.05	0.7	Warm	Yes
Coast	Medio Monte	Dry-hot	26	0.2626	0.028	1.2	Warm	Yes
Coast	Tapachula	Dry-hot	27	0.6059	<0.0001	1.9	Warm	Yes
Coast	Escuintla	Dry-hot	27	0.5386	0.000	3.3	Warm	Yes

Coast	Salvación	Dry-hot	25	0.3778	0.001	2.3	Warm	
Coast	Medio Monte	Wet	26	0.5173	0.000	1.1	Warm	Yes
Coast	Tapachula	Wet	27	0.7001	<0.0001	1.2	Warm	Yes
Coast	Escuintla	Wet	27	0.4543	0.003	2.1	Warm	Yes
Coast	Plan de Iguala	Wet	26	0.4562	0.001	1.5	Warm	
Coast	Salvación	Wet	26	0.6964	<0.0001	3.6	Warm	

SM Table V. Changes in monthly rainfall between 1990 and 2016 in the Sierra Madre, Central Depression (CD) and Coast areas of Chiapas, Mexico. Only weather stations with significant ($p<0.05$) rainfall trends are included. Significant rainfall trends during the longer 1960-2016 period at the same stations are indicated in the far-right column (Trend since 1960), where data are available since 1960. Details of these trends are shown in SM table VI.

Area	**Weather Station**	**Month**	**No. of data**	**Regression value**	**P-value**	**Change (mm)**	**Trend since 1960**
CD	Francisco I. Madero	June	26	0.4036	0.002	200	
CD	Villa Corzo	Aug	17	0.4004	0.002	160	
CD	Francisco I. Madero	Sept	25	0.3475	0.002	220	
CD	Chicomuselo	Sept	24	0.2314	0.018	260	
CD	Benito Juárez	Aug	25	0.1852	0.021	180	
Sierra	Finca A. Prusia	May	18	0.277	0.003	200	No
Sierra	Buenos Aires	May	21	0.2848	0.010	150	
Sierra	Finca A. Prusia	June	18	0.2232	0.031	230	No
Sierra	Independencia	June	23	0.4194	0.000	440	
Sierra	San Jerónimo	June	25	0.2243	0.018	500	No
Sierra	Finca A. Prusia	July	18	0.2692	0.023	400	No
Sierra	San Jerónimo	July	24	0.2778	0.004	500	No
Sierra	Finca A. Prusia	Aug	18	0.1242	0.041	400	No
Sierra	Independencia	Aug	24	0.2366	0.031	320	
Sierra	San Jerónimo	Aug	24	0.2286	0.035	400	No
Sierra	Independencia	Sept	23	0.2495	0.002	400	
Sierra	San Jerónimo	Sept	23	0.3234	0.006	650	No
Sierra	San Jerónimo	Oct	25	0.2541	0.012	470	No
Coast	San Isidro	June	23	0.3693	0.001	400	
Coast	Talismán	Aug	20	0.2549	0.021	250	No
Coast	Metapa de Domínguez	Sept	24	0.4361	0.002	600	Yes

SM Table VI. Significant ($p<0.05$) trends in mean daily temperature and monthly rainfall during the periods of 1960-1989 and 1960-2016 at climate stations with significant trends during the 1990-2016 period, where data are available since 1960 in the regions of Pacific Chiapas.

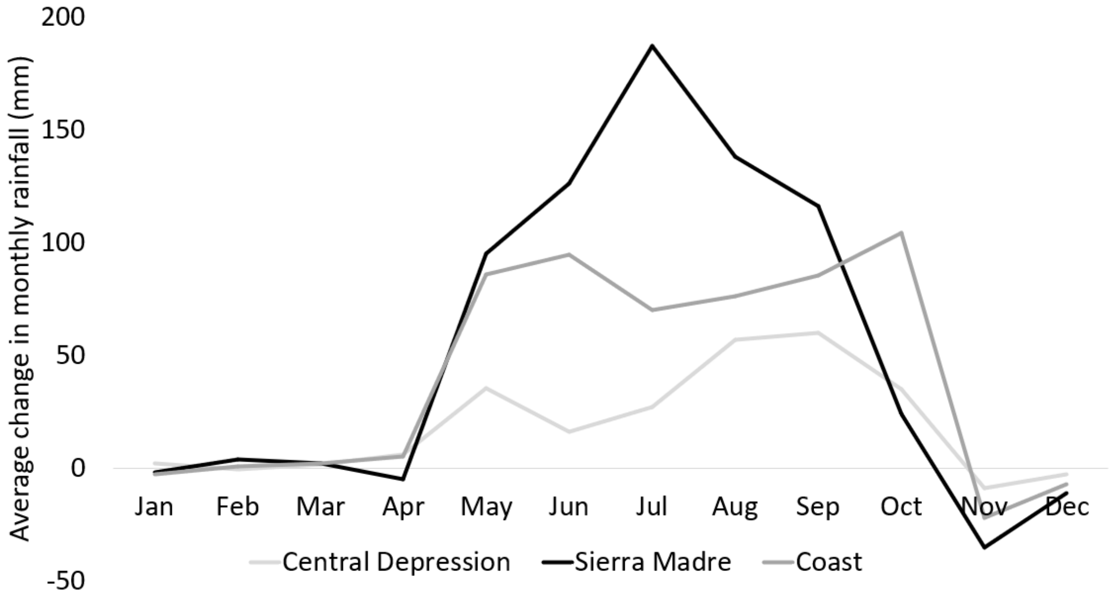
Mean Daily Temperature Trends 1960-1989/1960-2016							
Weather Station	**Season/ Month**	**Period**	**No. of data**	**Reg. value**	**P-value**	**Change (°C)**	**Trend**
Guadalupe Grijalva	Dry-cool	1960-2016	54	0.1925	0.001	-1.6	Cool
Guadalupe Grijalva	Dry-hot	1960-1989	29	0.2994	0.001	-1.9	Cool
El Progreso	Dry-cool	1960-2016	57	0.0687	<0.0001	1.8	Warm
El Progreso	Dry-hot	1960-1989	30	0.4865	<0.0001	-1.9	Cool
Frontera Amatenango	Dry-cool	1960-1989	30	0.7776	<0.0001	5.3	Warm
Tapachula	Dry-cool	1960-2016	57	0.7538	<0.0001	5.2	Warm
Tapachula	Dry-hot	1960-2016	57	0.6872	<0.0001	4.8	Warm
Tapachula	Wet	1960-2016	57	0.773	<0.0001	4.6	Warm
Escuintla	Dry-cool	1960-1989	30	0.2315	0.011	1.5	Warm
Escuintla	Dry-cool	1960-2016	57	0.1313	0.002	1.3	Warm
Escuintla	Dry-hot	1960-2016	57	0.0544	0.040	0.9	Warm
Escuintla	Wet	1960-2016	57	0.1029	0.008	1.0	Warm
Ignacio López Rayón	Dry-cool	1960-1989	29	0.414	0.001	1.2	Warm
Ignacio López Rayón	Dry-cool	1960-2016	56	0.1284	0.027	-0.9	Cool
Ignacio López Rayón	Dry-hot	1960-2016	56	0.5215	<0.0001	-2.3	Cool
Ignacio López Rayón	Wet	1960-2016	56	0.4717	<0.0001	-1.5	Cool
Pijijiapan	Dry-cool	1960-1989	30	0.2979	0.017	1.3	Warm
Pijijiapan	Dry-cool	1960-2016	57	0.482	<0.0001	1.7	Warm
Pijijiapan	Dry-hot	1960-2016	57	0.0942	0.020	0.6	Warm
Medio Monte	Dry-cool	1960-1989	30	0.3287	0.001	0.8	Warm
Medio Monte	Dry-cool	1960-2016	57	0.4819	<0.0001	1.2	Warm
Medio Monte	Dry-hot	1960-1989	30	0.2458	0.006	-0.9	Cool
Medio Monte	Dry-hot	1960-2016	57	0.3215	0.000	1.7	Warm
Medio Monte	Wet	1960-2016	57	0.6236	<0.0001	1.6	Warm
Monthly Rainfall Trends 1960-1989/1960-2016						**(mm)**	
Metapa de Domínguez	Sept	1960-2016	53	0.031	0.1527	310	Wet

SM Table VII. Years with data used to determine significant rainfall trends in the Central Depression: (1) Francisco I. Madero (June), (2) Francisco I. Madero (Sept), (3) Villa Corzo (Aug), (4) Chicomuselo (Sept), (5) Benito Juárez (Aug); Sierra Madre: (6) Finca A. Prusia (May), (7) Finca A. Prusia (June), (8) Finca A. Prusia (July), (9) Finca A. Prusia (Aug), (10) Buenos Aires (May), (11) Independencia (June), (12) Independencia (Aug), (13) Independencia (Sept), (14) San Jerónimo (June), (15) San Jerónimo (July), (16) San Jerónimo (Aug), (17) San Jerónimo (Sept), (18) San Jerónimo (Oct); and Coast: (19) San Isidro (June), (20) Talismán (Aug), (21) Metapa de Domínguez (Sept).

	Years with data where significant rainfall trends were determined																				
	Central Depression					Sierra Madre													Coast		
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1990	■		■		■					■	■	■	■	■	■	■	■	■	■	■	■
1991		■	■	■	■	■	■	■	■		■	■	■	■	■	■	■	■	■	■	■
1992	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
1993	■	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
1994	■	■	■	■	■					■	■	■		■	■	■	■	■	■	■	■
1995	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
1996	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
1997	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
1998	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
1999	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
2000	■	■		■	■	■	■	■	■		■	■	■	■	■	■	■	■	■	■	■
2001	■	■	■		■	■	■	■	■			■	■	■	■	■	■	■	■	■	■
2002	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■
2003	■	■	■	■	■						■	■	■	■	■	■	■	■	■	■	■
2004	■	■		■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
2005	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■	■	■	■
2006	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
2007	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
2008	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■
2009	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■
2010	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■
2011	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■		■
2012	■	■		■	■	■	■	■	■	■	■			■				■	■		
2013	■	■		■						■	■	■	■	■	■	■	■		■	■	■
2014	■	■		■	■					■	■	■	■					■			■
2015				■										■	■	■	■	■	■		■
2016				■																	

SM Table VIII. The mean and standard deviation of Normalized Difference Vegetation Index (NDVI), Potential Evapotranspiration (PET), and estimation of Estimation (ET) values within the Central Depression, Sierra Madre, and Coast regions of Chiapas, Mexico, during the transition from wet to dry, dry, and wet season of 1990, 2005, and 2020.

Region	**Season**	**NDVI**	**PET (mm/day)**	**ET estimation (mm/day)**
Central Depression	1990 transition	0.49±0.19	3.80±0.15	2.33±0.92
	1990 dry	0.35±0.14	5.39±0.26	2.31±0.94
	1990 wet	0.65±0.16	4.81±0.20	3.87±0.97
	2005 transition	0.56±0.19	3.66±0.16	2.54±0.83
	2005 dry	0.35±0.16	5.30±0.25	2.27±1.00
	2005 wet	0.68±0.16	4.63±0.16	3.89±0.91
	2020 transition	0.59±0.22	3.49±0.21	2.52±0.95
	2020 dry	0.42±0.17	5.20±0.33	2.69±1.11
	2020 wet	0.72±0.19	4.42±0.26	3.93±1.03
Sierra Madre	1990 transition	0.72±0.14	3.30±0.36	2.94±0.69
	1990 dry	0.64±0.17	4.51±0.51	3.58±0.99
	1990 wet	0.71±0.15	4.27±0.39	3.75±0.89
	2005 transition	0.75±0.12	3.10±0.40	2.89±0.62
	2005 dry	0.63±0.16	4.30±0.55	3.36±0.97
	2005 wet	0.74±0.15	4.62±0.16	3.59±0.82
	2020 transition	0.81±0.12	2.88±0.45	2.89±0.62
	2020 dry	0.71±0.15	4.08±0.60	3.57±0.91
	2020 wet	0.77±0.19	3.60±0.57	3.43±1.01
Coast	1990 transition	0.64±0.21	3.09±0.21	3.09±0.88
	1990 dry	0.49±0.20	5.07±0.28	3.11±1.15
	1990 wet	0.68±0.17	4.76±0.27	4.03±0.92
	2005 transition	0.70±0.19	3.76±0.20	3.27±0.79
	2005 dry	0.52±0.21	4.93±0.26	3.24±1.14
	2005 wet	0.70±0.18	4.57±0.27	4.01±0.90
	2020 transition	0.68±0.23	3.68±0.25	3.14±0.95
	2020 dry	0.60±0.23	4.78±0.31	3.58±1.21
	2020 wet	0.77±0.19	4.36±0.36	4.19±0.93



SM Figure 1. Regional averages of changes in monthly rainfall (mm) between 1990-2016 in the Central Depression, Sierra Madre and Coast regions of Chiapas Mexico.

CAPÍTULO 3. Climate trends, a hurricane, and phenological patterns in El Triunfo cloud forest, Mexico

Table S1. Tree species tagged for phenological observation in the El Triunfo Biosphere Reserve (Polygon 1) during 2019-2021. Species listed are in order of number of trees tagged. Species with asterisk were also observed in 1991-1993 by Solórzano et al. (2000). Abbreviations of species names are in parenthesis.

Family	**Scientific name**	**Local common name**	**No. of trees tagged**
Species producing feeding resources for quetzals			
Chloranthaceae	**Hedyosmum mexicanum* (*H mex*)	Muñeco	16
Lauraceae	**Nectandra rudis* (*N rud*)	Aguacatillo	15
Lauraceae	**Ocotea chiapensis* (*O chi*)	Tepeaguacate	15
Moraceae	**Trophis cuspidata* (*T cus*)	Aretillo	15
Moraceae	**Eugenia capuli* (*E cap*)	Escobillo	15
Rosaceae	**Prunus brachybotrya* (*P bra*)	Cacho de carnero	13
Melastomataceae	**Conostegia volcanalis* (*C vol*)	Uva	8
Moraceae	**Morus insignis* (*M ins*)	Mora	8
Lauraceae	**Licaria excelsa* (*L exc*)	Canelillo	7
Verbenaceae	**Citharexylum mocinnii* (*C moc*)	Perla	7
Mysinaceae	**Ardisia compressa* (*A com*)	Chime	6
Lauraceae	**Ocotea acuminatissima* (*O acu*)	Canelillo	5
Mysinaceae	*Ardisia verapazensis* (*A ver*)	Chime	5
Rhamnaceae	**Frangula capreifolia* (*F cap*)	Canzucar	4
Actinidiaceae	**Saurauia madrensis* (*S mad*)	Moquillo rojo	4
Theaceae	**Symplococarpun purpusii* (*S pur*)	Palo Colorado	3
Lauraceae	**Cinnamomum zapatae* (*C zap*)	Canelillo	3
Clusiaceae	*Clusia salvinii* (*C sal*)	Palo de agua	2
Araliaceae	*Dendropanax arboreus* (*D arb*)	Cerillo	2
Rosaceae	**Prunus tetradenia* (*P tet*)	Cochoc	1
Species producing fruits which quetzals could potentially consume (without observation)			
Actinidiaceae	*Saurauia yasicae* (*S yas*)	Moquillo blanco	4

Table S2. Correlations between climate variables, minimum daily temperature (Tmin), mean daily temperature (Tmean), maximum daily temperature (Tmax), monthly rainfall and solar radiation, and reproductive phenophases in the zoochorous community of the cloud forest of El Triunfo, Mexico. Values are Spearman correlation coefficients and the P-value in parenthesis. Significant ($p<0.05$) values are in bold.

Phenophase	**Climate variable**					
	Tmin	**Tmean**	**Tmax**	**Rainfall**	**Daylength**	**Solar rad.**
Flowers						
No. ind.	**-0.64 (0.006)**	**0.65 (0.004)**	-0.46 (0.066)	**-0.51 (0.036)**	**-0.59 (0.013)**	0.10 (0.694)
No. sp.	**-0.68 (0.003)**	**-0.66 (0.004)**	-0.44 (0.076)	**-0.50 (0.043)**	**-0.58 (0.014)**	0.13 (0.614)
Intensity	**-0.71 (0.005)**	**-0.61 (0.016)**	-0.42 (0.094)	**-0.50 (0.045)**	**-0.54 (0.025)**	0.24 (0.332)
Unripe fruits						
No. ind.	-0.43 (0.082)	-0.47 (0.056)	-0.44 (0.079)	-0.31 (0.231)	-0.45 (0.072)	-0.23 (0.371)
No. sp.	**-0.49 (0.046)**	**-0.51 (0.038)**	**-0.49 (0.047)**	-0.20 (0.437)	**-0.53 (0.030)**	-0.35 (0.164)
Intensity	**-0.51 (0.037)**	-0.48 (0.053)	**-0.50 (0.042)**	-0.05 (0.841)	**-0.51 (0.036)**	**-0.52 (0.033)**
Ripe fruits						
No. ind.	0.06 (0.815)	0.22 (0.394)	0.28 (0.268)	-0.11 (0.673)	0.27 (0.291)	**0.61 (0.009)**
No. sp.	-0.19 (0.471)	-0.02 (0.951)	0.11 (0.687)	-0.28 (0.281)	-0.01 (0.971)	**0.56 (0.020)**
Intensity	0.17 (0.493)	0.32 (0.199)	0.40 (0.110)	-0.04 (0.868)	0.36 (0.155)	**0.64 (0.011)**
No. fruits	-0.03 (0.891)	0.05 (0.829)	0.14 (0.576)	-0.27 (0.281)	0.07 (0.784)	**0.52 (0.037)**
Biomass	-0.29 (0.243)	-0.16 (0.530)	-0.10 (0.681)	-0.34 (0.176)	-0.21 (0.428)	0.37 (0.144)

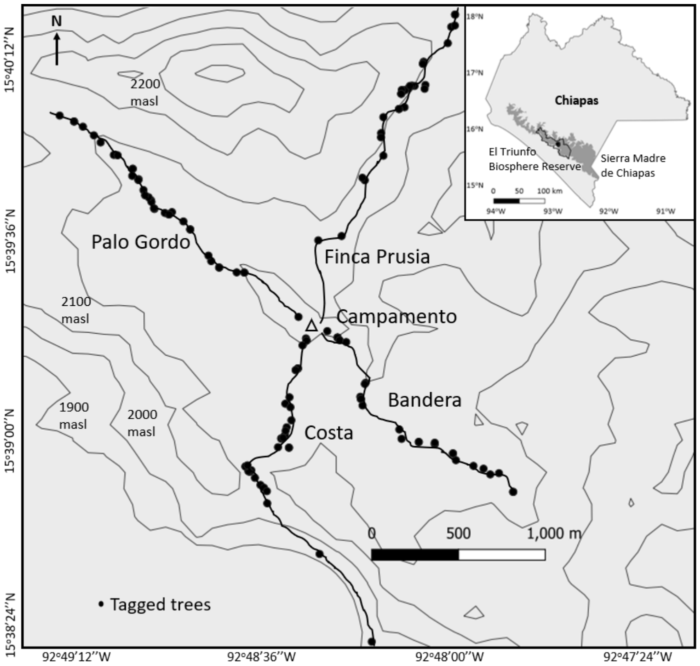
Table S3. Correlations between climate variables, minimum daily temperature (Tmin), mean daily temperature (Tmean), maximum daily temperature (Tmax), monthly rainfall and solar radiation, and reproductive phenophases of individual tree species within the zoochorous community in the cloud forest of El Triunfo, Mexico. Values are Spearman correlation coefficients and the P-value in parenthesis. Significant (p<0.05) values are in bold. Only significant (p<0.05) values are shown. Full species names of the abbreviations are in Table S1.

	Tmin	**Tmean**	**Tmax**	**Rainfall**	**Daylength**	**Solar radiation**
Flower intensity						
N rud	-0.46 (0.07)	-0.53 (0.03)	-	-0.60 (0.01)	-	-
T cus	-	-	-	-0.51 (0.04)	-	-
F cap	-	-	-	-0.48 (0.05)	-	-
A com	-0.71 (<0.01)	-0.61 (0.01)	-	-0.60 (0.01)	-0.50 (0.04)	-
S mad	-0.48 (0.05)	-	-	-	-	-
M ins	-0.77 (<0.01)	-0.81 (<0.01)	-0.83 (<0.01)	-	-0.83 (<0.01)	-0.49 (0.04)
C moc	-0.81 (<0.01)	-0.81 (<0.01)	-0.78 (<0.01)	-	-0.84 (<0.01)	-
O chi	-	-	-	-	-	-0.51 (0.04)
C vol	-0.80 (<0.01)	-0.82 (<0.01)	-0.67 (<0.01)	-0.48 (0.05)	-0.82 (<0.01)	-
Unripe fruit intensity						
N rud	0.56 (0.02)	0.47 (0.06)	-	0.45 (0.07)	0.42 (0.09)	-
T cus	0.61 (<0.01)	0.65 (<0.01)	0.62 (<0.01)	0.55 (0.02)	0.72 (<0.01)	-
P bra	-	-	-	-	-	-0.52 (0.03)
A com	-	-	0.63 (<0.01)	-	-	-
A ver	-	-	-	-	-	-0.58 (0.02)
E cap	-	-	0.55 (0.02)	-	-	-
C zap	-0.53 (0.03)	-	-0.47 (0.06)	-	-0.52 (0.03)	-
S mad	-0.58 (0.02)	-0.62 (0.01)	-0.71 (<0.01)	-	-0.72 (<0.01)	-
M ins	-0.60 (0.01)	-0.70 (<0.01)	-0.70 (<0.01)	-0.54 (0.02)	-0.66 (<0.01)	-
H mex	-	-0.58 (0.01)	-0.61 (<0.01)	-	-0.55 (0.02)	-
C moc	-0.79 (<0.01)	-0.84 (<0.01)	-0.71 (<0.01)	-0.65 (<0.01)	-0.77 (<0.01)	-
C vol	-0.55 (0.02)	-0.55 (0.02)	-0.61 (<0.01)	-	-0.67 (<0.01)	-
Ripe fruit intensity						
P bra	-0.47 (0.06)	-	-	-0.68 (<0.01)	-	054 (0.02)
F cap	0.69 (<0.01)	0.73 (<0.01)	0.61 (<0.01)	0.60 (0.01)	0.76 (<0.01)	-
A com	0.58 (0.01)	0.62 (0.01)	0.61 (<0.01)	-	0.67 (<0.01)	-
A ver	-0.50 (0.04)	-0.63 (0.01)	-0.75 (<0.01)	-	-0.72 (<0.01)	-0.70 (<0.01)
L exc	-0.52 (0.03)	-	-	-0.45 (0.07)	-	0.50 (0.04)
M ins	-	-	-	-0.63 (<0.01)	-	0.65 (<0.01)
H mex	-	-	-	-0.59 (0.01)	-	0.69 (<0.01)
C moc	-	-	-	-	-	0.76 (<0.01)
O chi	-	0.46 (0.06)	-	-	-	-
C vol	-	-	0.55 (0.02)	-	0.50 (0.04)	0.77 (<0.01)
Number of ripe fruits						
P bra	-0.72 (<0.01)	-0.66 (0.01)	-0.68 (<0.01)	-0.51 (0.04)	-0.74 (<0.01)	-
F cap	0.68 (<0.01)	0.72 (<0.01)	0.57 (0.02)	0.58 (0.01)	0.77 (<0.01)	-
A com	0.61 (0.01)	0.68 (<0.01)	0.66 (<0.01)	-	0.70 (<0.01)	-
A ver	-	-	-	-	-	-0.77 (<0.01)
L exc	-0.45 (0.07)	-	-	-	-	-
M ins	-	-	-	-0.61 (0.01)	-	0.68 (<0.01)
H mex	-0.44 (0.08)	-	-	-0.66 (0.01)	-	0.59 (0.02)
C moc	-	-	-	-	-	0.62 (0.01)
C vol	-	-	0.49 (0.04)	-	-	0.71 (<0.01)
Biomass of ripe fruits						
P bra	-0.73 (<0.01)	-0.64 (<0.01)	-0.71 (<0.01)	-0.45 (0.07)	-0.70 (<0.01)	-

F cap	0.68 (<0.01)	0.72 (<0.01)	0.57 (0.02)	0.58 (0.01)	0.77 (<0.01)	-
A com	0.61 (<0.01)	0.69 (<0.01)	0.66 (<0.01)	0.43 (0.08)	0.72 (<0.01)	-
A ver	-	-0.57 (0.02)	-0.73 (<0.01)	-	-0.70 (<0.01)	-0.77 (<0.01)
L exc	-0.45 (0.07)	-	-	-	-	-
M ins	-	-	-	-0.62 (<0.01)	-	0.68 (<0.01)
H mex	-	-	-	-0.66 (<0.01)	-	0.59 (0.02)
C moc	-	-	-	-	-	0.62 (0.01)
C vol	-	-	0.49 (0.04)	-	-	0.71 (<0.01)

Table S4. Number of fruits (total) estimated for each species each month from March 2019-May 2021 in the El Triunfo Biosphere Reserve, Chiapas, Mexico. Full species names of the abbreviations are in Table S1.

	2019								2020				2021					Average
Species	Mar	Apr	May	Jun	Aug	Sep	Oct	Dec	Jan	Feb	Mar	Dec	Jan	Feb	Mar	Apr	May	Biomass
H. mex	971	990	592	239	6	0	25	17	911	1911	2568	263	348	669	1010	392	345	32.0
N. rud	0	0	0	0	0	703	2030	3981	3327	3482	443	0	0	0	0	0	0	8.1
O. chi	7379	3778	522	460	1826	1204	1399	526	1190	653	600	575	6	7	14	36	13	18.6
T. cus	4549	4750	0	0	0	17540	3967	52	0	0	0	0	0	0	0	0	0	0.6
E. cap	37	37	0	0	0	0	895	1470	136	155	49	0	0	0	0	0	0	0.7
P. bra	7939	10033	3196	582	27	0	8670	14515	23522	25474	5675	3032	10382	3712	5771	2258	554	3.2
C. vol	2845	3111	1851	1609	434	444	0	0	133	9244	2260	3	41	883	466	2402	3291	0.5
M. ins	385	385	0	0	0	0	0	0	0	18	11387	2	0	0	18	23	0	2.2
L. exc	0	0	0	0	123	0	0	650	927	420	203	8	0	3	38	40	13	5.0
C. moc	120350	68225	13526	9723	0	0	0	0	44000	70675	65395	0	1925	2235	9252	35600	10919	0.6
A. com	332	540	910	86	316	488	103	0	7	0	6	1	0	20	0	16	26	0.8
O. acu.	0	0	0	0	0	0	0	0	73	50	9	0	0	0	0	0	0	2.1
A. ver	0	0	0	0	0	11	144	970	115	6	0	55	12	3	6	0	0	0.8
F. cap	0	0	3505	9420	6	0	0	0	0	0	0	0	0	0	0	566	972	0.6
S. mad	1080	1080	1672	633	0	0	0	0	275	242	762	62	101	170	45	221	3170	1.5
S. pur	0	0	0	0	0	0	0	0	0	0	0	0	0	115	0	0	0	6.1
C. zap	0	0	0	0	0	0	0	0	0	426	5617	0	0	0	0	0	0	0.9
C. sal	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	NA
D. arb	0	0	0	0	0	0	0	0	0	0	6817	0	0	0	0	5194	945	0.5
P. tet	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	NA
S. yas	0	0	0	0	222	190	55	0	0	0	0	0	0	12	0	0	0	1.5



SI Figure 1. Study area in the cloud forest of polygon 1, El Triunfo Biosphere Reserve, Chiapas, Mexico.

SM Table 1. Tree species, the average biomass of a fruit without seeds (g), and the lower diameter at breast height (DBH; cm) limit of trees producing fruits of each species, included in the study of community fruit production of quetzal feeding resources in El Triunfo Biosphere Reserve, Chiapas, Mexico.

Family	**Scientific name**	**Biomass of fruit (no seeds) (g)**	**DBH lower limit of mature trees (cm)**
Actinidiaceae	*Saurauia madrensis*	1.5	10
Actinidiaceae	*Saurauia yasicae*	1.5	7
Araliaceae	*Dendropanax arboreus*	0.5	13
Araliaceae	*Oreopanax sp.*	N/A	10
Chloranthaceae	*Hedyosmum mexicanum*	32.0	12
Clusiaceae	*Clusia salvinii*	N/A	10
Lauraceae	*Cinnamomum zapatae*	0.6	38
Lauraceae	*Licaria excelsa*	3.0	11
Lauraceae	*Nectandra rudis*	3.3	15
Lauraceae	*Ocotea chiapensis*	12.3	21
Lauraceae	*Ocotea acuminatissima*	1.1	N/A
Melastomataceae	*Conostegia volcanalis*	0.5	9
Moraceae	*Eugenia capuli*	0.3	4
Moraceae	*Morus insignis*	2.2	26
Moraceae	*Trophis cuspidata*	0.5	5
Mysinaceae	*Ardisia compressa*	0.7	10
Mysinaceae	*Ardisia verapazensis*	0.7	3
Rhamnaceae	*Frangula capreifolia*	0.5	N/A
Rosaceae	*Prunus brachybotrya*	1.8	22
Rosaceae	*Prunus tetradenia*	N/A	N/A
Theaceae	*Symplococarpun purpusii*	2.0	12
Verbenaceae	*Citharexylum mocinnii*	0.5	17

SM Table 2. Density of tree species (number of ind/ha), overall tree basal area (m^2/ha), and frequency between plots of species producing the feeding resources of the quetzal in polygon 1 of El Triunfo, Chiapas, Mexico.

Species	**Ind/ha**	**Basal area (m^2/ha)**	**Frequency**
Conostegia volcanalis	38.4	1.09	67.9
Eugenia capuli	34.8	0.31	47.2
Hedyosmum mexicanum	31.1	1.45	66.0
Symplococarpun purpusii	18.7	0.63	50.9
Trophis cuspidata	7.4	0.44	35.8
Ardisia compressa	5.5	0.23	28.3
Clusia salvinii	5.2	0.03	34.0
Saurauia madrensis	5.0	0.12	35.8
Nectandra rudis	4.7	0.64	32.1
Oreopanax sp.	4.5	0.03	18.9
Ocotea chiapensis	3.9	0.78	22.6
Saurauia yasicae	3.5	0.02	11.3
Prunus brachybotrya	2.1	0.27	11.3
Dendropanax arboreus	2.0	0.07	0.2
Licaria excelsa	2.0	0.02	11.3
Ardisia verapazensis	1.0	0.01	5.7
Citharexylum mocinnii	0.8	0.04	7.5
Morus insignis	0.5	0.08	7.5
Cinnamomum zapatae	0.1	0.01	1.9
Species within the study area but not present within plots			
Frangula capreifolia	Open light areas in central camp		
Prunus tetradenia	Not common in study area		
Ocotea acuminatissima	Mostly in small groups, but not common		