UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

Centro de Investigaciones en Ecosistemas

“LA INTERACCIÓN DE *HELICONIA* CON SUS INSECTOS HERBÍVOROS Y HONGOS PATÓGENOS FOLIARES EN SELVAS TROPICALES FRAGMENTADAS”

TESIS

QUE PARA OBTENER EL GRADO ACADÉMICO DE

DOCTOR EN CIENCIAS

PRESENTA

BRÁULIO ALMEIDA SANTOS

TUTOR PRINCIPAL DE TESIS: DRA. JULIETA BENÍTEZ MALVIDO

COMITÉ TUTOR: DR. FRANCISCO J. ESPINOSA GARCÍA
DR. MAURICIO R. QUESADA AVENDAÑO

MÉXICO, D.F. **ENERO, 2011**

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UNAM POSGRADO
Ciencias Biológicas

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

Por medio de la presente me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 17 de enero del 2011, se acordó poner a su consideración el siguiente jurado para el examen de DOCTOR EN CIENCIAS del alumno **BRÁULIO ALMEIDA SANTOS** con número de cuenta **508451157,** con la tesis titulada: **"La interacción de Heliconia con sus insectos herbívoros y hongos patógenos foliares en selvas tropicales fragmentadas"**, bajo la dirección de la **Dra. Julieta Benítez Malvido.**

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Sin otro particular, quedo de usted.

Atentamente
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, D.F., a 2 de marzo del 2011.

M del Coro Arizmendi
Dra. María del Coro Arizmendi Arriaga
Coordinadora del Programa

c.c.p. Expediente del interesado

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A Eva Warren Coraciara Stadtler

ÍNDICE

RESUMEN GENERAL

La deforestación y fragmentación de selvas tropicales constituyen uno de los principales motores de la crisis global de biodiversidad y servicios ecosistémicos. Aunque los cambios en la abundancia y distribución de las especies en selvas fragmentadas son bien conocidos, hay muy poca información sobre la alteración de interacciones bióticas claves para el funcionamiento del sistema. Interacciones antagonistas como planta-herbívoro y planta-patógeno son particularmente poco conocidas. En esta tesis se evaluó cómo la interacción de herbáceas del género *Heliconia* con sus insectos herbívoros y hongos patógenos foliares es afectada en fragmentos de selva y en la vegetación secundaria que se regenera en la matriz de un paisaje fragmentado del sureste de México (Chajul, Chiapas). Como preámbulo, se determinó la diversidad de especies nativas de *Heliconia* en el área de estudio y se hizo una síntesis global de los herbívoros y patógenos que atacan al género *Heliconia*. La hipótesis central que se probó fue que la perturbación humana, al aumentar la disponibilidad de luz en el sistema, favorecer la proliferación de plantas pioneras con pocas defensas contra herbívoros y patógenos, reducir el flujo génico entre las poblaciones de plantas hospederas, y favorecer la introducción de nuevos herbívoros y patógenos, aumenta la susceptibilidad de las plantas a daños bióticos. La predicción que se deriva de esa hipótesis general es que plantas en hábitats alterados presentarán mayores niveles de daño foliar que plantas en hábitats perturbados naturalmente (claros naturales) o no-perturbados (sotobosque de selva madura continua). Los principales resultados indican que la región de Chajul alberga una alta diversidad de heliconias nativas (ocho especies en un área de menos de 100 km^2), con una alta variedad de características morfológicas, ecológicas y de historia de vida. El género *Heliconia* es atacado por más de 150 especies de herbívoros y patógenos, de las cuales la mayoría son insectos folívoros y hongos patógenos foliares de

reconocido interés agrícola que atacan un amplio grupo de plantas no-relacionadas taxonómicamente. En las especies estudiadas, *H. latispatha*, *H. collinsiana* y *H. aurantiaca*, no hubo evidencia de que la perturbación humana aumenta los niveles totales de daños por insectos folívoros. Sin embargo, en los hábitat alterados por humanos (i.e. bordes de carretera, zonas riparias degradadas y fragmentos de selva pequeños) los herbívoros generalistas (hormigas cortadoras, *Atta cephalotes*) fueron favorecidos en detrimento de aquellos más especializados (algunos crisomélidos y orugas de Lepidoptera). En áreas donde los herbívoros generalistas fueron abundantes (bordes de carretera y fragmentos de selva), el daño causado por los generalistas compensó aquél causado por los especialistas, manteniendo el nivel total de daño foliar similar entre hábitats alterados por el hombre y hábitats perturbados naturalmente o no-perturbados. Aunque el daño por patógenos foliares varió mucho de planta a planta dentro de un mismo hábitat, hubo una clara tendencia de aumento en los niveles de daño por patógenos en los bordes de carretera, vegetación riparia y fragmentos de selva en comparación a sus respectivos controles. No fue posible encontrar un único mecanismo físico o biológico responsable de las diferencias en los patrones de herbivoría. Hubo evidencias de que se debieron a cambios en el microclima y en la calidad y densidad de hospederos (dureza de las hojas, cantidad de taninos foliares condensados, y densidad de vástagos en un radio de 10 m), pero la cantidad de área foliar removida varió consistentemente sólo con la abundancia de los herbívoros, muy probablemente debido a cambios positivos o negativos en el control descendente de sus poblaciones por depredadores y parasitoides. Los datos provenientes del monitoreo de *H. aurantiaca* por casi dos años en el sotobosque de fragmentos y de selva continua sugieren, que los niveles de herbivoría no tienen un efecto negativo sobre el crecimiento, sobrevivencia y reproducción de la planta hospedera, lo que es una señal positiva para el aprovechamiento de este género tolerante a la herbivoría en hábitats alterados. Se concluye que la perturbación humana altera las interacciones *Heliconia*-herbívoro y *Heliconia*-patógeno y que la producción de heliconias en bosques secundarios y degradados puede ayudar a conciliar conservación de biodiversidad y servicios ecosistémicos con desarrollo económico y social.

ABSTRACT

Deforestation and forest fragmentation are among the major drivers of the current global crisis of biodiversity and environmental services. Although the changes in species abundance and distribution in fragmented forests are well known, there is little information on how species interactions that are critical for ecosystem functioning can be altered in fragmented forests. Antagonistic interactions such as plant-herbivore and plant-pathogen are especially poorly known. In this thesis I evaluated how the interaction of the *Heliconia* herbs with their insect herbivores and leaf fungal pathogens is affected in forest fragments and secondary vegetation regenerating in the matrix of a fragmented landscape in Southern Mexico (Chajul, Chiapas). As a preamble, I determined the diversity of native *Heliconia* species in the study area and did a global synthesis about the herbivores and pathogens attacking the *Heliconia* genus. The central hypothesis I tested was that human disturbance, by increasing light availability in the ecosystem, favoring the proliferation of pioneer plants that are poorly defended against herbivores and pathogens, reducing gene flow among remaining host plant populations, and favoring the introduction of novel herbivores and pathogens, result in increased host plant susceptibility to biotic damage. The prediction derived from this hypothesis is that plants in human disturbed habitats will show greater levels of foliar damage than plants in natural disturbed (treefall gaps) or undisturbed habitats (understory of continuous forest). The main findings indicated that the region of Chajul homes a high diversity of native heliconias (eight species in less than 100 km^2), which are greatly variable in morphology, ecology and life history. The *Heliconia* genus is attacked by more than 150 herbivore and pathogen species; the huge majority is folivorous insects and leaf fungal pathogens with recognized agricultural importance that attack a broad group of taxonomically unrelated plants. In the species studied, *H. latispatha*, *H.*

collinsiana y *H. aurantiaca*, there was no evidence supporting the human-induced increase of total levels of herbivore damage. However, in human disturbance habitats (i.e. road edges, degraded riparian zones, and forest fragments), generalist herbivores (leaf-cutting ants *Atta cephalotes*) were favored in detriment of those more specialized (some crisomelids and caterpillars). In areas where generalists were abundant (road edges and forest fragments), the damage caused by generalists overcame the damage caused by specialists, leaving total levels of foliar damage similar between human disturbed habitats and natural disturbed or undisturbed habitats. Although the levels of pathogen damage varied greatly from plant to plant within the same habitat, there was a clear tendency of increase in total levels of pathogen damage in road edges, riparian vegetation and forest fragments compared to their respective controls. It was not possible to identify a single biological or physical mechanism underlying the patterns of herbivory. There was evidence that they were caused by microclimatic shifts and changes in host availability and quality (leaf toughness, condensed foliar tannins, density of conspecific shoots in a 10 m radius), but the amount of insect damage varied consistently only with the local abundance of herbivores, possibly due to positive and negative changes in top-down control of their predators and parasitoids. Data from a 2-yr monitoring of *H. aurantiaca* in the understory of forest fragments and continuous forest suggest that the levels of folivory has no significant effect on plant growth, survival, and reproduction, which represents a positive sign for the management of this herbivory-tolerant ornamental genus in human disturbed habitats. I concluded that human disturbance alters the *Heliconia*-herbivore and *Heliconia*-pathogen interactions and that the environmental-friendly production of heliconias in secondary and degraded tropical forests can help to combine socioeconomic development and the conservation of biodiversity and ecosystem services.

INTRODUCCIÓN GENERAL

Deforestación y fragmentación de selvas tropicales

La creciente demanda por energía, alimento y recursos naturales de una población global de casi siete mil millones de personas ha sido la principal causa de lo que se conoce actualmente como la “sexta extinción masiva” o “el evento de extinción del holoceno” (Wake & Vredenburg 2008). Los bosques templados fueron los primeros a ser convertidos en ciudades y campos agrícolas, y actualmente las selvas tropicales son uno de los biomas más vulnerables del planeta (Achard et al. 2002, FAO 2009). Se estima que la tasa actual de extinción de especies es 100 a 1000 veces mayor que el promedio histórico registrado para el período pre-humanos (Pimm et al. 1995, Myers 1997). Los efectos negativos de este rápido empobrecimiento biológico ya se empiezan a hacer visibles alrededor del mundo a través de la pérdida de servicios ecosistémicos esenciales para el bienestar humano (Reid et al. 2005, Duffy 2009, Nelson et al. 2010, Pereira et al. 2010).

La importancia de las selvas tropicales en la actual crisis global de biodiversidad y servicios ecosistémicos reside principalmente en el gran número de especies que albergan y en la gran cantidad de servicios que proveen (Corlett & Primack 2006, Lewis 2006). Estas selvas ocupan aproximadamente 10% de la superficie terrestre del planeta pero albergan entre 50 y 75% de sus especies (Lewis 2006 y referencias citadas). Las actividades humanas que han llevado a la destrucción de casi la mitad del área original cubierta por selvas tropicales varían de acuerdo a factores económicos, sociales, culturales y religiosos (Pimm & Raven 2000, Reid et al. 2005). En la mayoría de los países Neotropicales, por ejemplo, se produce carne y leche bovina en gran escala para atender a consumidores nacionales e internacionales, lo que ha llevado la ganadería extensiva a volverse un negocio multibillonario en la región, así como a la deforestación de extensas áreas (Laurance & Peres 2006, Steinfeld et al. 2006).

El resultado del uso indiscriminado de las selvas tropicales son paisajes fragmentados representados por un mosaico de fragmentos de selva, bosques secundarios, sistemas agrícolas, áreas urbanizadas, carreteras y una variedad de otros hábitats alterados. Estos mosaicos representan actualmente por lo menos la mitad de los trópicos (ITTO 2002), pero siguen teniendo un papel importante como reservorios de biodiversidad y proveedores de algunos servicios ecosistémicos (Chazdon et al. 2009, Dent & Wright 2009, Lugo 2009), por lo que deben ser considerados tanto en la conservación como en el manejo de las selvas tropicales. Uno de los retos para los científicos actuales interesados en ese tema es transcender la etapa del diagnóstico biológico de los ecosistemas alterados, i.e. del conteo de individuos y especies, y empezar a entender el funcionamiento y a identificar usos potenciales de comunidades biológicas remanentes que puedan ayudar a disminuir la presión humana sobre las pocas áreas de selvas continuas que aún existen. El estudio de las interacciones bióticas entre especies de niveles tróficos distintos (e.g. planta-herbívoro, planta-polinizador, depredador-presa) constituye una manera de evaluar el funcionamiento de hábitats alterados. La información ecológica básica generada en dichos estudios puede entonces ser utilizada en la elaboración de prácticas de manejo que contribuyan para la conservación ambiental y desarrollo económico y social de las comunidades que dependen o viven en las selvas fragmentadas.

En las últimas tres décadas un gran número de trabajos ha demostrado cómo y por qué los fragmentos de selva pierden especies y servicios ecosistémicos (Fahrig 2003, Laurance et al. 2011). La pérdida de hábitat inherente al proceso de fragmentación forestal reduce el área disponible para los diferentes grupos de organismos y aísla sus poblaciones.

Para un gran número de especies el aislamiento entre los fragmentos aumenta las tasas de endogamia (Young et al. 1996), resultando en una reducción del tamaño poblacional debido a la baja adecuación de las progenies (Keller & Waller 2002). Sin embargo, ésta parece no ser la principal causa del deterioro de las poblaciones dentro de los fragmentos en selvas tropicales (Harper et al. 2005, Tabarelli et al. 2008, Laurance et al. 2011). En selvas perennifolias, los "efectos de borde" en general se caracterizan por la pérdida de humedad en el ambiente, intolerancia fisiológica de muchas especies a ese desecamiento y, por consiguiente, cambios en la manera cómo las especies se distribuyen e interactúan (Murcia 1995). Los "efectos de borde" varían mucho en el tiempo y espacio (generalmente son más severos en los primeros 100 m del borde; Laurance et al. 2002), pero tienden a dominar fragmentos pequeños (<10 ha) o irregulares (alta relación perímetro:área) e inducen la biota remanente a un rápido proceso de degradación (Santos et al. 2008, 2010; Tabarelli et al. 2008, Lopes et al. 2009). Otros factores como la cacería, la tala selectiva, el fuego y el cambio climático actúan sinergísticamente con los efectos de borde, área, forma y aislamiento y determinan la magnitud de las pérdidas biológicas en los fragmentos de selva (Tabarelli et al. 2004, Ewers & Didham 2006, Laurance & Useche 2009).

Un componente fundamental de los paisajes fragmentados es la matriz que circunda los parches remanentes de hábitat (Kupfer et al. 2006), pero pocos estudios han sido realizados en esta área en comparación a los que se han realizados dentro de los parches (e.g. Gascon et al. 1999, Ricketts 2001, Nascimento et al. 2006, Dixo & Metzger 2010, Kennedy et al. 2010, Kuefler et al. 2010). Una de las razones de la escasez de estudios en la matriz de los paisajes fragmentados está relacionada con el principal marco conceptual utilizado para el desarrollo de la ecología de hábitats fragmentados: la teoría de biogeografía de islas, inicialmente propuesta por MacArthur & Wilson (1967) y luego modificada por Brown & Kodric-Brown (1977). Esta teoría utiliza las tasas de colonización y extinción de especies, así como métricas de área y aislamiento de islas oceánicas de origen volcánico para predecir el número de especies que dichas islas pueden mantener. Si uno interpreta selvas fragmentadas como un archipiélago de islas con distintos tamaños y grados de aislamiento, entonces dicha teoría puede ser de gran utilidad para identificar qué tanto se puede deforestar y aislar selvas tropicales de manera que su biodiversidad no sea alterada significativamente. Esta pregunta se la hicieron Thomas Lovejoy y colaboradores pocos años después de la modificación de la teoría de la biogeografía de islas por Brown & Kodric-Brown (1977), y a fines de la década de 1970 dieron inicio al mayor experimento de fragmentación de selvas tropicales del que se tiene registro (Proyecto Dinámica Biológica de Fragmentos Forestales, PDBFF, o BDFFP en inglés; ver detalles en Bierregaard et al. 1992).

Aunque los resultados de este experimento han sido fundamentales para el desarrollo de la ecología de selvas tropicales fragmentadas (Debinski & Holt 2000), cuarenta años después se sabe que el marco conceptual sobre el cual está fundamentado no se aplica para las selvas estudiadas (Laurance 2008). La teoría asume que el número de especies inicial en la isla oceánica es cero (i.e. la colonización es proceso dominante inmediatamente después de su creación); las especies son equivalentes ecológicamente (neutralidad a nivel de especies); la matriz − el océano − es impermeable para la biota terrestre de la isla; y las islas no sufren efectos de borde ni de otras fuentes de perturbación humana como la cacería, la tala selectiva, el fuego y la contaminación (DeSouza et al. 2001, Laurance 2008). Actualmente ya se sabe que todos esos supuestos son violados en los “archipiélagos” de selvas: los fragmentos de selva tienen la diversidad teórica máxima en el tiempo cero (i.e. son selvas maduras al momento de la fragmentación y la extinción es el proceso dominante en las fases iniciales); las especies tienen distintas probabilidades de colonización y extinción local de acuerdo a sus atributos de historia de vida; algunas especies tienen capacidad de hacer uso de la matriz, incluso de volverse hiperabundantes en esa zona respecto a su hábitat original; y los efectos de borde y de las otras fuerzas de origen humano son comunes en selvas fragmentadas (Laurance 2008).

Este avance empírico en la ecología de selvas fragmentadas ha demostrado la existencia de muchos factores extrínsecos a los parches remanentes que influyen su dinámica biológica, lo que ha aumentado el interés por la dinámica espacial y temporal de la matriz y ha llevado al desarrollo reciente de la ecología de paisajes fragmentados (Turner 1989, Levin 1992, Metzger 2001, Burel & Baudry 2003). Aunque la importancia ecológica de la matriz es ahora considerada en varios estudios sobre selvas fragmentadas, su relevancia para la conservación sigue siendo poco explorada. Si bien la matriz no alberga la diversidad biológica de la biota original ni la totalidad de sus servicios ecosistémicos, sus componentes no pueden ser ignorados en los planes de conservación y manejo (Tscharntke et al. 2005, Gardner et al. 2009). Particularmente, la vegetación secundaria que se regenera tras el abandono de campos de cultivo y potreros, así como a lo largo de cercas vivas, bordes de caminos, carreteras y zonas riparias modificadas, pueden ayudar a aumentar la conectividad entre los parches remanentes, proteger los suelos, reciclar nutrientes, almacenar carbono, mantener la función de los mantos acuíferos y mitigar la extinción de especies (Lugo 2009). Además, estos hábitats alterados pueden ser manejados con el objetivo de aumentar las fuentes de ingreso para comunidades rurales e indígenas que dependen directamente de ellos, y por consiguiente, disminuir la probabilidad de desmonte futuro (Harvey et al. 2008).

Herbivoría y enfermedades foliares en selvas fragmentadas

Los herbívoros y patógenos son fuerzas evolutivas esenciales para la diversificación de la vida y de las estrategias de defensa de las plantas (Coley & Barone 1996, Dangl & Jones 2001, Gilbert 2002, Kessler & Baldwin 2002, Núñez-Farfán et al. 2007, Burdon & Thrall 2009). Al afectar diferencialmente el crecimiento, sobrevivencia, y reproducción de las plantas hospederas, y por consiguiente la estructura poblacional de éstas y la manera cómo interactúan con otras plantas, los herbívoros y patógenos favorecen la coexistencia de especies de plantas con distintas historias de vida e influyen las trayectorias sucesionales y la resiliencia del ecosistema (Marquis 2005, Bradley et al. 2008, Wirth et al. 2008). Sus efectos pueden, por lo tanto, ser observados en todos los niveles de organización biológica, de genes a ecosistema. No obstante, hay muy poca información sobre estos tipos de interacciones bióticas en selvas tropicales fragmentadas, ya sea en la vegetación original remanente o en la matriz del paisaje fragmentado (Benítez-Malvido et al. 1999, Laurance 2005, Benítez-Malvido & Lemus Albor 2006).

La mayoría de los estudios realizados dentro de los parches remanentes de selva se ha enfocado en los cambios espaciales o temporales en la abundancia y distribución de los organismos tras la fragmentación. Lo poco que se ha estudiado en términos de interacciones bióticas se ha concentrado principalmente en interacciones mutualísticas como la polinización y la dispersión de semillas (Ghazoul 2005, Laurance 2005), cuya integridad también es fundamental para mantener el funcionamiento del ecosistema. Según Ruiz-Guerra et al. (2010), sólo 16 trabajos han evaluado la interacción planta-herbívoro en fragmentos de hábitat. Este número excluye a los estudios diseñados específicamente para evaluar los efectos de bordes, que suman alrededor de 55 (Wirth et al. 2008). En total, se tiene registro de sólo 71 estudios sobre la interacción planta-herbívoro en hábitats fragmentados, los cuales incluyen evidencias empíricas colectadas en selvas tropicales, bosques templados, plantaciones de pino y otros ecosistemas. Si se utiliza como referencia el número total de estudios con la expresión "*habitat fragmentation*" presentado por Fahrig (2003) (ca. 1600), los estudios sobre la interacción planta-herbívoro representan menos del 5% del conocimiento científico que se ha generado en hábitats fragmentados[1].

Pocas conclusiones pueden ser sacadas de lo que se sabe hasta la fecha, pero hay por lo menos una de particular interés para el avance de la ecología de interacción planta-herbívoro en selvas fragmentadas. Las evidencias indican que los herbívoros generalistas como cérvidos (Alverson et al. 1998), homópteros (Ozanne et al. 2000), ortópteros (Knight & Holt 2005) y hormigas cortadoras (Wirth et al. 2007) generalmente se favorecen en parches dominados por efectos de borde en detrimento de aquellos más especializados como lepidópteros e insectos minadores y formadores de agallas (Wirth et al. 2008; ver también Myers 1997 y Stork et al. 2009). Las causas del favorecimiento de los generalistas cerca del borde parecen estar relacionadas con las condiciones microclimáticas favorables, aumento en la calidad y disponibilidad de las plantas hospederas e interrupción del control descendente de las poblaciones de herbívoros por depredadores y parasitoides (Wirth et al. 2008). Las posibles consecuencias de la proliferación de herbívoros generalistas incluyen el aumento en la velocidad de recambio de materia y energía, retraso en la regeneración de la comunidad debido a un efecto positivo sobre el reclutamiento de plantas pioneras típicas de

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[1] En 26 diciembre de 2010 el número de estudios conteniendo la expresión "habitat fragmentation" en el ISI Web of Science era de 4,315, lo que disminuiría el porcentaje de estudios sobre herbivoría para menos del 2%.

estadios iniciales de sucesión, reducción de la resiliencia del sistema y aumento del riesgo de extinciones en cascada (Wirth et al. 2008).

Sin embargo, todavía no se ha establecido adecuadamente la relación de causa y efecto entre la hiperabundancia de herbívoros generalistas y el deterioro de las poblaciones de plantas en selvas fragmentadas, sobre todo porque hay pocos estudios que evalúan el impacto de esos herbívoros sobre el desempeño de las plantas hospederas (e.g. Meyer et al. 2011). Particularmente, no sé sabe con exactitud si los herbívoros generalistas (1) realmente representan una amenaza adicional para la vegetación remanente, porque remueven más tejido foliar que los especialistas vulnerables localmente (ver Barbosa et al. 2005, Fonseca 2009); (2) si dañan cantidades similares de tejido foliar a las que dañaban los especialistas extintos localmente; o (3) si remueven menos tejido de lo que removían los especialistas. Para plantas con alta resistencia a la herbivoría como la mayoría de las especies de sucesión tardía, se esperaría que su desempeño se redujera en el primer caso debido al aumento en los niveles de daño foliar; se mantuviese constante en el caso donde los herbívoros generalistas dañan cantidades de tejido similares a las que dañaban los especialistas extintos localmente; o aumentase en el caso donde menos área foliar es dañada por los generalistas. La respuesta de plantas tolerantes a la herbivoría, como las pioneras típicas de claros naturales, sería más variable y dependería de su grado de tolerancia al daño. El entendimiento de las fuentes de variación en el daño relativo causado por herbívoros generalistas y especialistas podría ayudar a unificar los resultados discrepantes sobre los patrones de herbivoría en selvas fragmentadas descritos hasta el momento; actualmente no hay un consenso si la herbivoría aumenta, disminuye o permanece constante en los parches remanentes (ver Wirth et al. 2008 y Ruiz-Guerra et al. 2010). El estudio presentado en el capítulo 4 de esta tesis representa un esfuerzo pionero en la búsqueda de tal entendimiento.

Las enfermedades foliares infecciosas son un tema aún más desconocido en la literatura de selvas tropicales fragmentadas (Coley & Barone 1996, Benítez-Malvido & Lemus-Albor 2006), en gran medida debido a la histórica falta de comunicación entre ecólogos tropicales y fitopatólogos. Hasta la fecha se tiene registro de sólo dos estudios sobre el tema, uno desarrollado en las selvas altas perennifolias del sureste de México (Benítez-Malvido & Lemus-Albor 2005) y otro en la Amazonia Brasileña (Benítez-Malvido et al. 1999). En México el daño foliar por patógenos en plántulas leñosas fue tres veces mayor en el borde que en el interior de la selva (1.8% vs. 0.6% del área foliar), mientras que en Brasil estuvo poco relacionado con la disminución del tamaño del parche de selva. Aunque ninguna conclusión general puede ser sacada de estos dos trabajos, se espera que la incidencia de enfermedades foliares aumente en los fragmentos de selva debido a la proliferación de plantas pioneras con pocas defensas, condiciones microclimáticas favorables al desarrollo de algunas enfermedades, y al alto riesgo de introducción de nuevos patógenos tras la perturbación humana (Benítez-Malvido & Lemus-Albor 2006).

Las interacciones planta-herbívoro y planta-patógeno son igualmente desconocidas en los hábitats alterados que componen la matriz de las selvas tropicales fragmentadas. En el único estudio sobre el tema, Benítez-Malvido et al. (2005) evaluaron experimentalmente los niveles de daño por herbívoros en plántulas de tres especies de Sapotaceae trasplantadas a cuatro hábitats que representaban un gradiente de perturbación: potreros, bosques secundarios dominados por *Vismia* (ambos en la matriz), fragmentos de selva de 1 ha y selva madura continua. El daño por herbívoros fue consistentemente menor en los potreros para todas las especies, pero en *Pouteria caimito* y *Micropholis venulosa* el daño fue mayor en la selva continua que en los otros hábitats, mientras que en *Chrysophyllum pomiferum* el daño fue mayor en el bosque secundario que en los otros hábitats. Estos resultados contrastantes con plantas hospederas relacionadas taxonómicamente sugieren que el filtro ambiental creado por el hombre puede tener un papel más importante que las relaciones filogéneticas de las plantas en el establecimiento de relaciones planta-herbívoro en paisajes fragmentados (ver también Gómez et al. 2010). Dada la diversidad de parches de vegetación secundaria que se están regenerando en los trópicos, cada uno siguiendo trayectorias sucesionales distintas de acuerdo a la intensidad, frecuencia, duración, tipo de disturbio y distancia a la fuente de propágulos más cercano (Uhl 1982), es de esperarse una variación espacial considerable en cualquier tipo de interacción biótica que se establezca en la matriz de selvas fragmentadas. El capitulo 3 provee informaciones sobre cómo las interacciones planta-herbívoro y planta-patógeno pueden ser alteradas en bordes de carretera y zonas riparias degradadas en comparación a claros naturales en la selva continua.

El género *Heliconia*

El género *Heliconia* es el único de la familia Heliconiaceae, una de las ocho familias de monocotiledóneas del orden Zingiberales (Berry & Kress 1991). En México, sus representantes son conocidos popularmente como platanillo, huertilla o papatla. El género tiene distribución pantropical, pero sólo seis de las 180 especies descritas son nativas de los trópicos del Viejo Mundo (Berry & Kress 1991). Por lo general ocurren en altitudes menores que los 500 m, pero algunas pueden ser encontradas por encima de los 2,000 m (Berry & Kress 1991). La apariencia general de las heliconias es muy parecida a la de una platanera (de ahí el nombre platanillo), aunque algunas especies se parecen a otras

Zingiberales de las familias Cannaceae (e.g. *H. vaginalis*) y Zingiberaceae (e.g. *H. aurantiaca*). Las heliconias presentan un rizoma perenne con alta capacidad de almacenamiento de energía del cual periódicamente brotan nuevos vástagos, también descritos en la literatura como retoños, *ramets* o *shoots*. Los vástagos son de ciclo de vida corto, generalmente duran menos de tres años, y se reproducen una única vez. Luego, entran en un proceso gradual de senescencia hasta morirse y ser reemplazados por otros recién-producidos (Berry & Kress 1991).

En condiciones naturales, la mayoría de las especies sólo puede ser encontrada en áreas con alta disponibilidad de luz (e.g. claros naturales); sólo unas cuantas se han adaptado a la baja disponibilidad de luz del sotobosque sombreado (e.g. *H. aurantiaca*) (Stiles 1975, Berry & Kress 2001). La mayoría de las especies demandantes de luz tienen alta capacidad para propagarse horizontalmente a través de estolones, por lo que tienden a formar grandes agregados en hábitats alterados por los humanos[2]. De hecho, son consideradas malezas en algunas regiones donde su aprovechamiento es desconocido. Éste el caso de *H. latispatha* y *H. collinsiana* en la región de Chajul, Chiapas, que se vuelven muy abundantes tras la perturbación humana. Las heliconias que habitan en el sotobosque generalmente tienen muy limitada capacidad de propagación horizontal y difícilmente forman agregados. Por ejemplo, *H. aurantiaca* raramente presenta plantas con más de 10 vástagos (B. A. Santos, observación personal); lo mismo se observa en la especie

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[2] Seifert (1975) se refiere a los agregados de heliconias en floración como “islas ecológicas” para un gran número de especies de insectos que utilizan sus brácteas. Las islas de heliconias fueron utilizadas para probar algunas predicciones de la entonces novedosa teoría de la biogeografía de islas de MacArthur y Wilson (1967).

sudamericana tolerante a la sombra *H. acuminata* (Bruna 2003). La demografía de estas especies depende más bien de la germinación de semillas, producto de la polinización por colibríes, y del subsecuente establecimiento de plántulas.

Las especies neotropicales poseen inflorescencias muy grandes y coloridas, lo que ha provocado que las heliconias tengan un puesto privilegiado en el mercado internacional de plantas ornamentales (Criley 1991, Diaz et al. 2002). Hoy en día diversas especies de heliconias son cultivadas alrededor del mundo, incluso en países europeos (e.g. Holanda y Alemania) y asiáticos (e.g. Bangladesh) (Criley 1991, Sultana & Hassan 2008). Paradójicamente, pocos países tropicales saben cuántas especies nativas de *Heliconia* tienen y cuál es su distribución − Costa Rica y Colombia son ejemplos exitosos en ese sentido (Stiles 1975, Atehortua 1997). La mayoría de ellos, incluyendo a aquellos con tradición en botánica, aún carece de este tipo de información básica (e.g. México y Brasil). Además de lo llamativo de sus inflorescencias, las heliconias también son utilizadas por decoradores como plantas enteras en macetas o en paisajes de interior (Pancoast 1991). Sus largas hojas son utilizadas por comunidades indígenas y rurales para diversos fines como un sustituto para las hojas de plátano (e.g. envoltura de tamales centroamericanos). En Tailandia, las heliconias han sido utilizadas en el desarrollo de técnicas de tratamiento de aguas residuales (Sohsalam et al. 2008, Konnerup et al. 2009). Su uso farmacéutico también ha sido evaluado en la producción de sustancias antiofídicas que inhiben las actividades proteolítica, coagulante y hemolítica del veneno de las serpientes *Lachesis muta*, *Crotalus durissus cumanensis*, *Micrurus mipartitus* y *Bothropis asper* y *B. atrox* (e.g. Otero et al. 2000, Núñez et al. 2004, Pereañez et al. 2008, Estrada et al. 2010; Colombia lidera este tipo de investigación).

Varios ecólogos tropicales también han demostrado interés en las heliconias, principalmente debido a la comunidad de insectos que habitan sus hojas nuevas enrolladas y las brácteas que conforman sus inflorescencias. Los estudios empezaron por naturalistas tan temprano como en la década de 30 (Skutch 1933), pero ganaron proyección a partir de 1960 con la pregunta central en ecología acerca de cómo la competencia y la depredación estructuran las comunidades biológicas. Las hojas y brácteas de las heliconias fueron consideradas ecosistemas en los cuales habitaban diferentes comunidades de insectos. Para 1982 ya había una extensa revisión sobre la estructura y dinámica de las comunidades de insectos asociados a las heliconias (Seifert 1982), y la mayor parte de la evidencia generada sugería que la depredación era más importante que la competencia (Strong 1977, 1982). Concomitantemente, surgieron varios estudios acerca de la estrecha relación entre las heliconias y los colibríes que polinizaban sus flores (e.g. Stiles 1975, Temeles & Kress 2003). La evolución del territorialismo en colibríes, por ejemplo, parece estar relacionada a la adaptación de las heliconias a distintos tipos de hábitat (Linhart 1973, Stiles 1975). Las especies de *Heliconia* típicas de áreas sombreadas no tienen recurso (luz) suficiente para producir un gran número de flores y no forman grandes agregados debido a su baja capacidad de propagación horizontal, por lo que tampoco ofrecen recurso (néctar) suficiente para que un colibrí establezca un territorio en sus alrededores (Linhart 1973, Stiles 1975). Los colibríes ermitaños, generalmente con menor tamaño corpóreo, se especializaron en ese grupo de heliconias con inflorescencias pequeñas, las cuales, por lo menos en Costa Rica, florecen secuencialmente y así evitan competencia por polinizadores y/o hibridación (Stiles 1975). Las heliconias demandantes de luz, por otro lado, en hábitats abiertos disponen de suficientes recursos para producir grandes inflorescencias y una cantidad de flores suficiente para garantizar el establecimiento del territorio por los colibríes (Stiles 1975). Aunque esas heliconias garantizan el servicio de polinización, por general experimentan mayores tasas de endocruzamiento en comparación a las heliconias tolerantes a la sombra debido a la baja movilidad de polen entre individuos y poblaciones (Linhart 1973).

Más recientemente, la demografía y estructura genética de algunas especies de heliconias ha sido estudiada en condiciones naturales (e.g. *H. metallica* en Perú, Schleuning et al. 2009; *H. uxpanapensis* en México, Suárez-Montes et al. 2011). En términos demográficos, *H. acuminata* es la especie mejor conocida, pues viene siendo estudiada desde la década de 90 en un paisaje fragmentado de la Amazonia Brasileña. Los resultados sugieren que el estrés hídrico en los fragmentos de selva lleva a la pérdida de vástagos por planta, a la reducción en las tasas de crecimiento, y al aumento de la relación raíz:tallo (Bruna et al. 2002). Las poblaciones de los fragmentos están sesgadas hacia clases de tamaño menores, por lo que tienden a presentar un menor número absoluto de individuos reproductivos que aquél observado en la selva continua (Bruna & Kress 2002). Aunque ello no necesariamente lleva a una reducción en la producción y dispersión de semillas (Uriarte et al. 2010), la especie sufre reducciones significativas en la germinación de semillas y reclutamiento de plántulas en los fragmentos (Bruna 1999, 2002). Modelos matriciales proyectan un ligero deterioro de las poblaciones en los fragmentos (disminución de 1.0-1.5% por año vs. crecimiento de 2.3-4.0% por año en la selva continua) (Bruna 2003, Bruna & Oli 2005), pero los censos anuales en campo indican que las poblaciones crecen a tasas mayores que las teóricas tanto en los fragmentos como en la selva continua (Bruna 2003). En resumen, los estudios liderados por Emilio Bruna tras 30 años de fragmentación experimental en el Amazonas Central sugieren que *H. acuminata* sufre pocos cambios demográficos en fragmentos de selva. Un patrón similar parece observarse en el Sureste de

México con *H. aurantiaca*, uno de los equivalentes ecológicos de *H. acuminata* en Mesoamérica (B. A. Santos, observación personal), pero todavía no existe evidencia empírica que lo compruebe.

Las heliconias también han despertado el interés de los agrónomos y fitopatólogos, especialmente después del reconocimiento de las heliconias como plantas ornamentales y la introducción del plátano (*Musa*) a las Américas, pues algunas enfermedades de las plataneras utilizan las heliconias como hospederos alternativos (e.g. Madriz et al. 1991, Sewake & Uchida 1995, Connelly 1999, Assis et al. 2002, Lins & Coelho 2004, Hennen et al. 2005, Peña et al. 2006, Costa 2007, Serra & Coelho 2007, Chin et al. 2008, Santana et al. 2009a, b; Torre-Santana et al. 2010). Ejemplos son la bacteria *Ralstonia solanacearum* y diferentes especies del hongo *Fusarium*, que causan respectivamente el Moko y el Falso Mal de Panamá en los plátanos (Sabadell-González 2003, Wicker et al. 2007, Zoccoli et al. 2009). Algunos insectos especializados en *Heliconia* y otras pocas Zingiberales neotropicales expandieron su dieta hacia los plátanos introducidos. Orugas de Lepidoptera de la subfamilia Brassolinae (Nymphalidae), las mayores orugas de los Neotrópicos (DeVries 1987), en especial los géneros *Caligo* y *Opsiphanes*, se volvieron plagas en los platanales (Strong 1984). En un intento fallido de control químico de esos insectos, la aplicación del insecticida eliminó a las avispas que depredaban las orugas en lugar de erradicar a las orugas propiamente, resultando en un incremento en la densidad de orugas y mayores daños a la producción platanera (Strong 1984). El capítulo dos de esta tesis provee información más detallada acerca de las plagas y enfermedades de las heliconias.

En suma, la información generada por ecólogos, agrónomos, fitopatólogos, naturalistas, decoradores, jardineros y otros profesionistas interesados en las heliconias, en especial aquella relacionada con los herbívoros y patógenos de las heliconias, hacen de las heliconias uno de los mejores sistemas para estudiar las interacciones planta-herbívoro y planta-patógeno en los Neotrópicos. Con base en esa valiosa información y en el entendimiento de cómo la interacción *Heliconia*-herbívoro y *Heliconia*-patógeno puede ser alterada en selvas secundarias y degradadas, se puede generar directrices para su aprovechamiento sustentable en estos sistemas supuestamente “improductivos”.

OBJETIVO GENERAL

El objetivo general de esta tesis fue determinar cómo la interacción de herbáceas del género *Heliconia* con sus insectos herbívoros y hongos patógenos foliares es afectada en fragmentos de selva y en la vegetación secundaria que se regenera en la matriz de un paisaje fragmentado del sureste de México (Chajul, Chiapas).

Objetivos específicos

1. Determinar la diversidad de especies nativas de *Heliconia* del área de estudio y describir sus principales atributos ecológicos, morfológicos y de historia de vida (capítulo 1);
2. Sintetizar la información disponible sobre los herbívoros y patógenos que atacan al género *Heliconia*, incluyendo datos sobre su taxonomía, ecología e importancia agrícola (capítulo 2);
3. Evaluar cómo las interacciones *Heliconia*-herbívoro y *Heliconia*-patógeno cambian en la vegetación secundaria temprana que se regenera en bordes de carretera y zonas riparias degradadas en relación a claros naturales en la selva continua (capítulo 3);
4. Examinar posibles cambios en la interacción *Heliconia*-herbívoro en el sotobosque de fragmentos de selva en relación al sotobosque de la selva continua (capítulo 4);

5. Determinar si las tasas de infección por hongos patógenos foliares son mayores en el sotobosque de los fragmentos de selva que en la selva continua (capítulo 5).

CAPITULO I

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Research note

New records of *Heliconia* (Heliconiaceae) for the region of Chajul, Southern Mexico, and their potential use in biodiversity-friendly cropping systems

Nuevos registros de *Heliconia* (Heliconiaceae) para la región de Chajul, sur de México, y su uso potencial en plantaciones amigables de la biodiversidad

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Abstract. We report 4 new records of *Heliconia* species (Heliconiaceae) for the region of Chajul, one of the most studied sites of the Mexican Lacandona. Records are for *H. champneiana* Griggs cv. Maya Gold, *H. latispatha* Bentham cv. Orange Gyro, *H. vaginalis* Bentham, and *H. wagneriana* Petersen. We provide a brief description of morphological and ecological traits of the species and demonstrate the high potential they have to be cultivated in biodiversity-friendly cropping systems. We suggest the use of *Heliconia* in the enrichment of secondary forests and forest fragments as an alternative of combining forest management with biological conservation.

Key words: *Heliconia aurantiaca*, *Heliconia champneiana*, *Heliconia collinsiana*, *Heliconia latispatha*, *Heliconia librata*, *Heliconia spissa*, *Heliconia vaginalis*, *Heliconia wagneriana.*

Resumen. Se registran por primera vez 4 especies de *Heliconia* (Heliconiaceae) para la región de Chajul, uno de los sitios más estudiados de la lacandona mexicana. Los nuevos registros son para *H. champneiana* Griggs cv. Maya Gold, *H. latispatha* Bentham cv. Orange Gyro, *H. vaginalis* Bentham, y *H. wagneriana* Petersen. Se presenta una breve descripción acerca de las características morfológicas y ecológicas de las especies y se demuestra el alto potencial que tienen para ser cultivadas en plantaciones amigables de la biodiversidad. Se sugiere el uso de *Heliconia* en el enriquecimiento de bosques secundarios y fragmentos de selva como una alternativa de combinar manejo forestal con conservación biológica.

Palabras clave: *Heliconia aurantiaca*, *Heliconia champneiana*, *Heliconia collinsiana*, *Heliconia latispatha*, *Heliconia librata*, *Heliconia spissa*, *Heliconia vaginalis*, *Heliconia wagneriana.*

Heliconiaceae is a plant family represented by a unique tropical genus, *Heliconia*. These perennial herbs belong to the order Zingiberales and are phylogenetically close to Musaceae, Strelitziaceae, Marantaceae, Cannaceae, Zingiberaceae, and Lowiaceae (Berry and Kress, 1991). *Heliconia* traditionally belonged to Musaceae with the genera *Musa* and *Ensete*. The unique combination of inverted flowers, presence of a single staminode, and peachlike fruits led taxonomists to place *Heliconia* into a new family, Heliconiaceae Nakai. The overwhelming majority of the 180 known species of *Heliconia* are in the Neotropics, while only 6 are native to the Old World tropics, especially from Samoa in the Pacific Ocean to the Indonesian island of Sulawesi (Berry and Kress, 1991).

Heliconia interacts with a vast number of organisms in tropical forests. Hummingbirds pollinate their colorful flowers in the Neotropics, while bats pollinate their pale green flowers in the Paleotropics (Berry and Kress, 1991). Fruits are blue in the Neotropics and red in the Paleotropics, but both are dispersed by many bird species (Berry and Kress, 1991). Viruses, bacteria, and fungi are known to infect their roots, shoots, leaves, inflorescences, fruits, and seeds (Assis et al., 2002). A myriad of insects including flies, hispine and flattened carabid beetles, caterpillars, and ants feed on or live inside their water-filled floral bracts and young rolled leaves (Seifert, 1982). Such biotic interactions involving *Heliconia* demonstrates its ecological value in tropical communities.

Heliconia is also an important ornamental genus. It has been long commercialized in European and American

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markets as cut flowers, potted plants, and in interior landscape. To give an example, Hawaiian *Heliconia* production generated about 2.8 million dollars between 1987 and 1988 with a production of 370 000 stems (Berry and Kress, 1991). In 2000 and 2001, Colombia exported 16 species, cultivars, and varieties of *Heliconia* to 44 countries, with incomes reaching about 440 million dollars (Diaz et al., 2002). Both Hawaiian and Colombian *Heliconia* where produced in small cultivation areas (<1 km^2 for Hawaii), indicating how these plants can maximize the use of space. Despite their ecological and economic values, geographic distribution of native *Heliconia* remains poorly understood in Mexico.

In this work we include 4 species of *Heliconia* that represent the first records for one of the most studied sites of the Mexican Lacandona: the Chajul Biological Station (16°08' N, 90°55' W) and its vicinity in the southern limit of the Montes Azules Biosphere Reserve (hereafter region of Chajul). Species were observed in the localities of Chajul (16°07' N, 90°55' W), Loma Bonita (16°06' N, 90°59' W), Playón (16°10' N, 90°53' W) and in both margins of the Lacantún River. A brief description of morphological and ecological traits of species is provided and its potential use in biodiversity-friendly cropping systems is discussed. New records were observed during a long-term research on *Heliconia*-pathogen-herbivore interaction.

To guarantee that findings were actually new records, we searched the recorded species in Berry and Kress (1991), Martínez et al. (1994), and Gutiérrez-Baéz (1996, 2000). These publications provide useful information on the botany and ecology of *Heliconia,* permit accurate species identification in the field, and join the available information on *Heliconia* distribution in Mexico. Because these studies are more than 10 years old, we used ISI Web of Science, Google Scholar, the Missouri Botanical Garden database (Mesoamerica projects), and the CONABIO database (World Biodiversity Information Network – REMIB) to search for recent records of *Heliconia* in Mexico. Since it is easy to identify reproductive individuals of *Heliconia* in the field (see Berry and Kress, 1991), no botanical collection was done. Nevertheless, species determination was also supported by specialists in Heliconiaceae (W. J. Kress) and by reviewing specimens in herbaria. Botanical nomenclature followed Berry and Kress (1991).

We found 8 species of *Heliconia* in the region of Chajul (Table 1). Four of them had already been listed by Martínez et al. (1994) and Gutiérrez-Baéz (1996) for the region of Chajul: *H. aurantiaca* Ghiesbreght ex Lemaire (Castillo 3688 – CHAPA, XAL), *H. collinsiana* Griggs var. *collinsiana* (Sinaca and Ibarra 1102 – MEXU, XAL; Castillo 3953 – XAL), *H. librata* Griggs (Sinaca and Ibarra 1093 – MEXU), and *H. spissa* Griggs cv. Mexico Red (Castillo 3779 – XAL). Our results highlight the occurrence of 4 other species in the same region: *H. champneiana* Griggs cv. Maya Gold (see Stevens 25585 – MO, Davidse 36370 – BRH, MO), *H. latispatha* Bentham cv. Orange Gyro (see Ibarra 265 – MO), *H. vaginalis* Bentham (see Breedlove 47357 – MO), and *H. wagneriana* Petersen (see Stevens 25115 – MO).

According to Kress (2001), *H. champneiana* is found from Southern Mexico to Nicaragua, but no detailed information on the species distribution in Mexico was provided. Here, we complement his data by demonstrating that the species is found in the region of Chajul, Chiapas. *Heliconia latispatha* occurs throughout the Neotropics, from Mexico to South America (Berry and Kress, 1991; Gutiérrez-Baéz, 2000). In Mexico, this species can be found in the states of Veracruz, Tabasco, Oaxaca, Campeche, and Chiapas (Gutiérrez-Baéz, 2000). In the state of Chiapas, particularly, there are records for the localities of Ostuacan, Tonalá, Escuintla, Yajalón, Tres Picos, Huixtla, and Tapachula (Gutiérrez-Baéz, 2000). We add the region of Chajul to this list. *Heliconia vaginalis* is found from Mexico to Colombia (Berry and Kress, 1991; Gutiérrez-Baéz, 2000). In Mexico, it has been recognized in Veracruz, Tabasco, Guerrero, and Chiapas. In Chiapas, there are records for Palenque, Ursulo Galván, La Libertad, and now for the region of Chajul. *Heliconia wagneriana* has the same distribution as *H. vaginalis* (from Mexico to Colombia) (Martínez et al., 1994; Berry and Kress, 1991), but in Mexico it has been only documented in Tacotalpa (Tabasco) and La Libertad (Chiapas) (Martínez et al. 1994; CONABIO database). We expand southward its distribution in Chiapas.

Expanding the geographic distribution of plant species in highly diverse tropical rain forests is a significant contribution toward the success of conservation initiatives. With accurate geographic distributions we are able to identify local biodiversity hotspots and conserve more species in smaller areas. Our bibliographic review revealed that the Mexican Lacandona houses 14 native species of *Heliconia* (*H. adflexa*, *H. aurantiaca*, *H. champneiana*, *H. collinsiana*, *H. dielsiana*, *H. latispatha*, *H. librata*, *H. psittacorum*, *H. rostrata*, *H. schiedeana*, *H. spissa*, *H. uxpanapensis*, *H. vaginalis*, and *H. wagneriana*). The region of Chajul, as defined here (~100 km^2), accounts for 57% (8 species) of this diversity in less than 1.5% of the Mexican Lacandona area (~8 000 km^2). This makes the region of Chajul a priority site for conservation of these ecologically and economically important plants.

Because of its high local diversity of *Heliconia*, the region of Chajul is a highly suitable site for the sustainable management of the genus in Mexico. Morphological differences in the inflorescences its 8 species confer a

Table 1. Morphological and ecological traits of eight native species of *Heliconia* recorded in the region of Chajul, Chiapas, Southern Mexico. Species descriptions were based on Berry and Kress (1991), Gutiérrez-Baéz (1996, 2000) and on our field observations. Asterisks represent new records for the region of Chajul

Species	*Height (m)*	*Growth habit*	*Inflorescence orientation*	*Bract arragement*	*No. of bracts*	*Bract color*	*Habitat*	*Blooming*
H. aurantiaca	0.5-2.0	zingiberoid	erect	Spiral	3-6	orange, with pale green tip	MF, FR, SF	Dec-Jun
*H. champneiana**	2.0-5.0	musoid	erect	Distichous	5-13	gold to yellow, green along distal keel and at tip	TG	Apr-Nov
H. collinsiana	1.7-5.5	musoid	pendent	Spiral	6-14	dark-red to orange-red	SF, TG, OA	All year
*H. latispatha**	1.7-5.5	musoid	erect	Spiral	7-17	orange	SF, TG, OA	All year
H. librata	1.3-3.3	musoid	erect	Distichous	11-18	yellow	MF, FR SF, TG	May-Dec
H. spissa	1.3-2.7	musoid	erect	Spiral	5-7	red or pink, greenish distally	FR	Feb-Sep
*H. vaginalis**	1.0-5.0	cannoid	erect	spiral or distichous	3-7	red to red-orange	MF, TG	Jun-Dec
*H. wagneriana**	1.7-5.0	musoid	erect	Distichous	6-20	colorful, from the keel to the cheek: green, yellow, and red	SF, TG, OA	Jan-Sep

MF= mature, old growth, continuous forests; FR= forest fragments; SF= early secondary forests (< 20 yrs old); TG= large, early treefall gaps embedded in the continuous forest; OA= open areas.

variety of cut flowers for the grower (Table 1). Successive periods of blooming guarantee production throughout the year (Table 1). Differences in growth habit and plant size give additional variety to the products to be commercialized as potted plants or in interior landscapes (Table 1). Such natural variety of ornamental products demonstrates the high potential of the region of Chajul for the market of ornamental plants.

Considering the ongoing scenario of deforestation and forest fragmentation in the Mesoamerican biodiversity hotspot, the major challenge for the conservationists is to design efficient strategies that combine species use with biodiversity conservation (Harvey et al., 2008). Mexican fragmented landscapes are usually dominated by small private fragments that still sustain a large subset of the original biota (Arroyo-Rodríguez et al., 2009). By encouraging the enrichment of forest fragments with native *Heliconia* species, we may add an economical value to forest remnants and increase the likelihood of their protection. Because the huge majority of *Heliconia* species are shade-intolerant, forest enrichment can be done without logging in natural treefall gaps. The same can be done in secondary forests that regenerate after the abandonment of unproductive agricultural lands. Nonetheless, growers should be technically assisted in order to maintain the genetic, functional and taxonomic diversity of the managed forests.

To summarize, few regions in the tropics have the local diversity of native *Heliconia* species that the region of Chajul has. Such biological heritage has potential to be rationally exploited through the implementation of biodiversity-friendly cropping systems, combining economical activities with nature conservation. Further studies should evaluate the use of *Heliconia* in disturbed forests from an economic perspective. Special attention should be paid to find potential consumers in the competitive internal and external markets of ornamental plants, especially in Europe and the USA, to identify logistic bottlenecks in the commercialization of these perishable products, such as costs of infrastructure and transportation toward distribution and sale centers, and to quantify financial benefits for local people in order to insure economic and social development for the region.

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CAPITULO II

RRH: Pests and diseases of *Heliconia*

Herbivores and pathogens of *Heliconia* and their implications for the management of these ornamental plants in secondary and degraded tropical forests

(Enviado a Biodiversity and Conservation)

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Abstract

The cultivation of the *Heliconia* ornamental plants in secondary and degraded forests has been recently recognized as a plausible solution to link socioeconomic development to biodiversity conservation. This biodiversity-friendly cropping system can fail, however, if cultivation is done with no background on the pests and diseases attacking these plants. Here we integrated taxonomic, ecological, and agricultural information of *Heliconia* herbivores and pathogens in order to identify how product quality could be jeopardized in secondary and degraded tropical forests. A total of 58 herbivores and 99 pathogens were recorded attacking *Heliconia* roots, rhizome, pseudostem, leaves, and/or inflorescences in Latin America, North America, Europe, Asia, and Australia. Herbivores included insects (> 85% of the species), arachnids, gastropods, and mammals. Pathogens were mostly represented by fungi (> 95%), but nematodes and one bacterium were also recorded. The proportion of species attacking the leaves was about five times greater than that attacking the attractive, profitable inflorescences (88% vs. 15%), representing a positive sign for the *Heliconia* management as cut flowers. Two thirds of the species were generalists (attacked *Heliconia* and non-Zingiberales species) and presented high ability to become widespread in the forests to be managed. Nevertheless, 82% of the species have been already reported attacking some agricultural crops, and for some of them there is information on their prevention, mitigation, and/or elimination. Our results encourage the commercial production of native *Heliconia* in human-dominated landscapes as an alternative to add economic value to secondary and degraded tropical forests and improve the effectiveness of conservation initiatives.

Keywords: forest fragmentation, herbs, non-timber forest product, secondary forest.

Introduction

Most of the tropical forests are currently represented by secondary and degraded forests highly variable in their capacity to provide ecosystem goods and services (ITTO 2002). These forests usually maintain only part of their function compared to primary forests, but even so they are able to protect soils, cycle nutrients, support wildlife, store carbon, maintain watershed function, and mitigate species extinction (Lugo 2009). At least in regions where large tracts of continuous primary forests are absent, conserving these altered forests is the only option for ensuring forest goods and services in the long term. A major issue is how to prevent unprotected secondary and degraded forests from being converted to pastures or agricultural fields. Increasing their economic value through the implementation of biodiversity-friendly cropping systems is a promising way of doing that, especially in regions with high social and economic differences where the majority of the remaining forests are private.

Ornamental plants with consolidated markets, but also with clear possibilities of being expanded, are of particular interest for conservation. This is the case for the banana-related tropical genus *Heliconia* (Heliconiaceae), which is cultivated and commercialized around the world as cut flowers, potted plants, and in interior landscapes (Berry and Kress 1991). Profits generated by *Heliconia* production are high. Hawaiian production generated about 2.8 million dollars between 1987 and 1988 with a production of 370,000 stems (Criley 1991). In 2000 and 2001, Colombia exported 16 species, cultivars, and varieties of *Heliconia* to 44 countries, with incomes reaching about 440 million dollars (Diaz et al. 2002). Nevertheless, few tropical countries do explore this valuable resource. To give a local example, the region of Chajul in Southern Mexico combines suitable climate, high local diversity of native *Heliconia* species, great variety among species in terms of growth habitat and inflorescence color and appearance, successive blooming peaks (some species bloom year-round), and high proximity to an important consumer (USA) (Santos et al. 2009). Despite this high potentiality for *Heliconia* production, *Heliconia* are treated as weeds in that region and eliminated with no use. A similar underutilization of these ornamental herbs is observed in many regions of Central and South America (Criley 1991). If we add the potential use of *Heliconia* in tropical medicine and ecological engineering (Otero et al. 2000, Núñez et al. 2004, Pereañez et al. 2008, Sohsalam et al. 2008, Konnerup et al. 2009, Estrada et al. 2010), its elimination is not recommended at all.

Commercial production of *Heliconia*, as any other plant cultivated in either biodiversity-friendly or conventional cropping systems, requires information on their potential pests and diseases. In the case of ornamental plants, biotic damages in their vegetative or reproductive parts can negatively affect product quality and therefore result in significant financial losses (Loges et al. 2005). Pests and diseases of *Heliconia* are relatively well-known (e.g. Sewake and Uchida 1995, Assis et al. 2002), but information is too scattered to provide general guidelines for the management of these plants in altered forests. In this study we summarized such information in order to identify how production and product quality could be jeopardized by herbivores and pathogens in secondary and degraded tropical forests. We first described major trends in biotic damage to assess which part of the plant is more likely to be damaged. Then, we integrated data on the ecology and agricultural/economic importance of the *Heliconia* herbivores and pathogens to predict potential changes in their spatial distribution in human-dominated landscapes. Finally, we inferred potential risks of *Heliconia* production in biodiversity-friendly cropping systems in secondary and degraded forests and suggested some techniques that could minimize them.

Methods

The genus *Heliconia* is pantropical and has more than 180 species described (Berry and Kress 1991). The huge majority of the species are native to South and Central America, only six species are native to the Old World tropics, from Samoa in the Pacific Ocean to the Indonesian island of Sulawesi (Berry and Kress 1991). To summarize the herbivores and pathogens reported to attack *Heliconia* we performed a comprehensive review using ISI Web of Science, Google Scholar, the fungal databases of the United States Department of Agriculture (Farr and Rossman 2010) and the pathogen database of the Pacific Island Ecosystems Research Center - US Geological Survey (USGS-PIERC 2010). We complemented our review with books, book chapters, MSc and PhD thesis, unpublished information, and technical reports. Each herbivore and pathogen species was classified according to its family, subclass, plant part they attack, major type of damage, range of hosts, and agricultural/economic importance.

The herbivores and pathogens were classified according to their range of hosts as specialist on Heliconiaceae, i.e. when the species attacks exclusively *Heliconia* species, specialist on Zingiberales, i.e. when the species attacks Heliconiaceae, Musaceae, Strelitziaceae, Marantaceae, Cannaceae, Zingiberaceae, and Lowiaceae, generalist, i.e. when the species attacks any *Heliconia* species and one or more non-Zingiberales species, and “unknown”, when no or little information about the host plants it attacks was available. The agricultural/economic importance of the *Heliconia* herbivores and pathogens was broadly defined as “yes”, “no”, or “unknown”. The category “yes” was assigned when any agricultural plant was among the hosts, category “no” was assigned when no host plant with agricultural importance was among the hosts, and “unknown” when agricultural relevance of the host plants was not clear. We are aware that this criterion is quite broad, but given the lack of detailed agricultural information for most of the herbivores and pathogens recorded, the classification is helpful. We used Chi-square tests to compare the proportion of species among the different categories of type of damage, number of plant parts attacked, range of hosts, and agricultural/economic importance of the herbivores and pathogens. Types of damage caused by less than 5% of the species were collapsed into the category "others" for the purposes of the analyses.

Results

We recorded a total of 58 herbivore and 99 pathogen species belonging to 55 families and 14 classes attacking the genus *Heliconia* (Table 1). Records were not restricted to the Neotropics (Latin America), the biogeographic region in which the huge majority of *Heliconia* species have evolved. Instead, records were reported in North America, Europe, Asia, and Australia. Most of the herbivores were insects (87.9%), but arachnids (*Brevipalpus*, *Raoiella*, *Tetranychus*) and mammals (*Atribeus*, *Thyroptera, Bos*, and Geomyidae) were also reported. All but five pathogen species reported were fungi. Non-fungal pathogens were represented by four nematode species belonging to three genera (*Helicotylenchus*, *Meloidogyne*, *Xiphinema*) and one species of bacterium (*Ralstonia solanacearum*). No attack by viruses was reported until now.

Most of the herbivore and pathogen species (68.1%) damaged only one plant part, but some caused damage to two or more host organs (15.9%), the rest of the species (16.0%) had no information on the damage type they cause. Leaves were attacked by 88.0% of the 133 species with known damage type, followed by vascular tissues (15.8%), inflorescences (15.0%), roots and rhizome (13.5%), and pseudostem (10.5%) (Fig. 1A, $\chi^2 = 206.1$, df = 4, $P < 0.0001$). The most common type of damage was leaf spots (43.6% of the 133 species), followed by defoliation (16.5%), leaf scrapping (13.5%), wilt and death (8.3%), sap depletion (6.8%), inflorescence spots (anthracnose included, 6.8%), root galls (3.0%), rust (2.3%), leaf roosting (made by bats, 1.5%), rhizome rot (0.8%), powdery mildew (0.8%), damping-off (0.8%), and pseudostem and rhizome boring (0.8%) (Fig. 1B, $\chi^2 = 91.2$, df = 6, $P < 0.0001$).

Around 65.5% of the 142 species with known hosts were classified as generalists, followed by specialists on Zingiberales (24.6%) and specialists on Heliconiaceae (9.8%) (Fig. 1C, $\chi^2 = 70.7$, df = 2, $P < 0.0001$). Of the 150 species with some information on their agricultural/economic importance, 82.0% have already been reported attacking agricultural crops (Fig. 1D, $\chi^2 = 60.2$, df = 1, $P < 0.0001$).

Discussion

Although the cultivation of native *Heliconia* species in secondary and degraded forests has been recognized as a potential bridge to combine socioeconomic development and nature conservation (Santos et al. 2009), to date there is no guidance for the management of their potential pests and diseases in such biodiversity-friendly cropping systems. Our comprehensive review from records in Latin America, North America, Europe, Asia, and Australia revealed more than 150 species of fungi, insects, arachnids, mammals, nematodes, and bacteria attacking the genus *Heliconia*. This global pool of potential pests and diseases is split into smaller groups at the local scale in which *Heliconia* production is carried out (see Assis et al. 2002, Costa 2007, and Sewake and Uchida 1995 for examples in Pernambuco [Brazil], Distrito Federal [Brazil] and Hawaii [USA]). Based on the available information we estimate that growers will handle no more than 30 potential pests and diseases in their *Heliconia* crops in altered forests, but further studies are needed to confirm this number.

Few records of herbivores and pathogens were reported for *Heliconia* in natural conditions because of the small number of studies on *Heliconia*-herbivore and *Heliconia*-

pathogen interactions in the wild (e.g. Auerbach and Strong 1981, Santos and Benítez-Malvido 2011). An exception should be done for the specialized hispine beetles, which have been extensively studied by biologists (e.g. Strong 1977a, b, Wilf et al. 2000, McKenna and Farrell 2005). These small beetles establish a commensalism-like interaction with their Zingiberales hosts, usually damaging less than 5% of the leaf area and representing small risk for *Heliconia* production. The limited knowledge about potential pests and diseases could generate quite uncertainty on the viability of *Heliconia* management in secondary and degraded tropical forests. However, evidence from the degraded Atlantic forest of Northeast Brazil indicates that the fungal pathogens that infect *H. psittacorum* in forest fragments also attack the herb in nearby greenhouses and small crop fields (e.g. *Colletotrichum gloesporioides*, *Cladosporium* sp., Assis et al. 2002, B. A. Santos et al. unpublished data). A similar pattern is observed in Costa Rica, where the common owl butterflies (Nymphalidae) have been found attacking many species of *Heliconia* in both managed and non-managed systems (Strong 1984, DeVries 1987). These studies suggest that the information generated in *Heliconia* agrosystems may be useful for the management of these herbs in altered forests (i.e. agroecological systems). Nevertheless, we suggest a rapid assessment of their major herbivores and pathogens prior to the implementation of the environmental-friendly cropping system. This can be easily done by evaluating the disease symptoms and insect feeding marks, by sampling insects associated with their foliage and inflorescences, and by inspecting banana plantations in areas abutting the managed forest (heliconias and bananas share many herbivores and pathogens, many with recognized agricultural importance, e.g. *Ralstonia solanacearum*, *Fusarium* spp., Assis et al. 2002, Watanabe 2007, Zoccoli et al. 2009).

The most attractive and profitable part of *Heliconia* − the inflorescence − was about five times less likely to be attacked by herbivores and pathogens than the vegetative parts (15% vs. 88% of the species). This broad pattern, which appears to hold at the local scale as well (see Sewake and Uchida 1995, Assis et al. 2002), constitutes an advantage for the *Heliconia* management as “cut flowers”. Foliage production for ornamental purposes is not encouraged due to the high number of species causing leaf spot, defoliation, or leaf scrapping, and the high product quality required by the international market of ornamental plants (Loges et al. 2005). Nevertheless, *Heliconia* leaves showing “unacceptable” levels of biotic damage for ornamental purposes could be locally commercialized as a surrogate for banana leaves, which have numerous culinary uses in many tropical countries.

The fact that around 90% of the herbivores and pathogens were not specialists on Heliconiaceae is not an advantage for *Heliconia* production in human-dominated forest landscapes because generalists are expected to proliferate after human disturbance (Wirth et al. 2008, Stork et al. 2009, see also Gilbert and Hubbell 1996, Benítez-Malvido and Lemus-Albor 2006). One of the main reasons for that is the prevalence of pioneer plants in degraded and secondary tropical forests (Tabarelli et al. 2010), which in general are poorly defended against herbivores and pathogens compared to shade-tolerant, slow-growing plant species typical of undisturbed forests (Coley and Barone 1996). This inconvenience, however, can be offset by feasible environmental-friendly techniques that prevent or mitigate potential outbreaks of generalist herbivores and pathogens. For instance, 82% of the *Heliconia* herbivores and pathogens were recorded attacking some agricultural crops, and for some of them there is information on pest/disease control. Much information could be imported from banana management in agroecological systems and combined to some recommendations made by Berry and Kress (1991), Assis et al. (2002) and Sewake and Uchida (1995) for the prevention, mitigation, and elimination of *Heliconia* pests and diseases in agrosystems. Actions such as using disease-free seeds, plantlets, and sterile soils during seedling production, maintaining good soil moisture in the field, eliminating and burning infected leaves and other sick organs, and removing insects (adults and larvae) by hand or with entomological net, could minimize the losses caused by biotic agents.

In summary, biodiversity conservation will not work without protecting the remaining pristine habitats, but also not without a recognition of the contribution of the "rest", i.e. forest fragments, secondary forests, abandoned fields and pastures and areas managed by agriculture and forestry (Tscharntke et al. 2005, Chazdon et al. 2009). The rational use of non-woody forest products such as the *Heliconia* ornamental herbs can add economic value to unprotected secondary and degraded tropical forests and therefore improve the effectiveness of conservation initiatives. Many tropical countries rich in native *Heliconia* species are currently dominated by human-disturbed forests and characterized by the underutilization of *Heliconia* resources. Although some *Heliconia* herbivores and pathogens may expand their area of distribution after forest disturbance and become potential pests and diseases, the use of environmental-friendly control techniques already known for some agricultural crops and *Heliconia* agrosystems could be modified and applied to the cultivation of *Heliconia* in degraded and secondary tropical forests.

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Figure legend

Figure 1. Proportion of herbivore and pathogen species attacking the genus *Heliconia* according to the plant part attacked (A), major type of damage (B), range of hosts (C), and agricultural/economic importance (D).

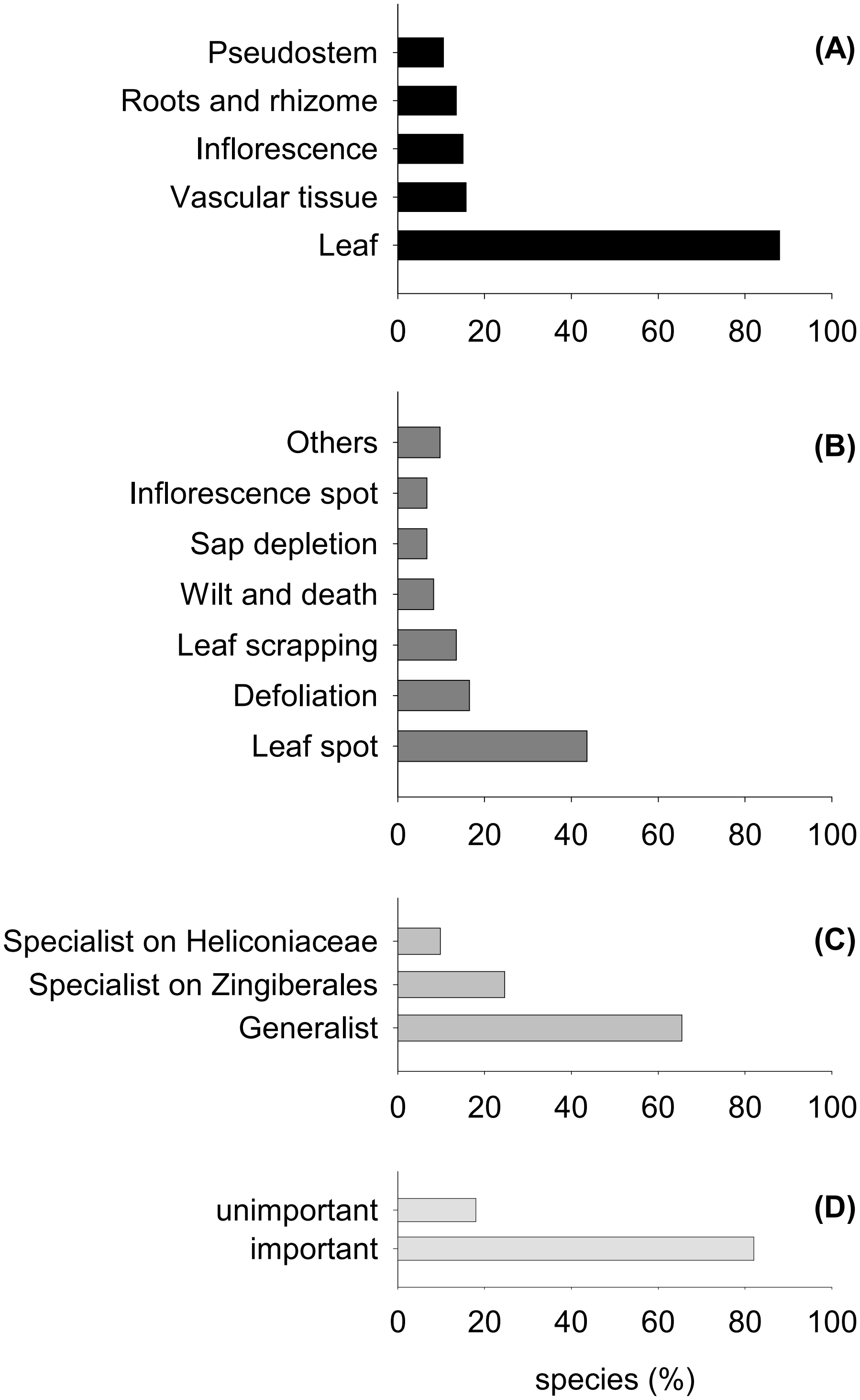
Pseudostem
Roots and rhizome
Inflorescence
Vascular tissue
Leaf
(A)
0
20
40
60
80
100
Others
Inflorescence spot
Sap depletion
Wilt and death
Leaf scrapping
Defoliation
Leaf spot
(B)
0
20
40
60
80
100
Specialist on Heliconiaceae
Specialist on Zingiberales
Generalist
(C)
0
20
40
60
80
100
unimportant
important
(D)
0
20
40
60
80
100
species (%)

Figure 1.

Table 1. Taxonomic and ecological characteristics of the herbivore and pathogen species attacking the genus *Heliconia*. A broad classification on their agricultural/economic importance is reported.

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Herbivores							
Acharia apicalis (= *Sibine apicalis*)	Limacodidae	Insecta	Leaves	Defoliation	Generalist	No	Auerbach and Strong 1981
Acharia cf. *stimulea* (= *Sibine* cf. *stimulea*)	Limacodidae	Insecta	Leaves	Defoliation	Generalist	No	Santos and Benítez-Malvido in press
Acharia sp. (= *Sibine sp.*)	Limacodidae	Insecta	Leaves	Defoliation	Generalist	No	Auerbach and Strong 1981
Aleurodicus disperses	Aleyrodidae	Insecta	Vascular tissue	Sap depletion	Generalist	Yes	Chin et al. 2008
Antichloris eriphia	Arctiidae	Insecta	Leaves	Defoliation	Generalist	Yes	Assis et al. 2002, Watanabe 2007
Antichloris sp.	Arctiidae	Insecta	Leaves	Defoliation	Generalist	Yes	Santos and Benítez-Malvido in press
Atribeus watsoni	Phyllostomidae	Chiroptera	Leaves	Leaf roosting	Generalist	No	Chaverri and Kunz 2006
Atta cephalotes	Formicidae	Insecta	Leaves	Defoliation	Generalist	Yes	Santos and Benítez-Malvido in press
Atta opaciceps	Formicidae	Insecta	Leaves	Defoliation	Generalist	Yes	Born et al. 2009
Atta sexdens sexdens	Formicidae	Insecta	Leaves	Defoliation	Generalist	Yes	Assis et al. 2002, Born et al. 2009
Bos sp.	Bovinae	Mammalia	Pseudostem and leaves	Defoliation	Generalist	Yes	B. A. Santos, pers. observ.
Brevipalpus sp.	Tenuipalpidae	Arachnidae	Leaves	Leaf spot	Generalist	Yes	Miranda et al. 2007
Caligo atreus dionysos	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	De Vries 1987
Caligo brasiliensis sulanus (= *Caligo eurilochus sulanus*)	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	De Vries 1987

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Caligo illioneus oberon	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	De Vries 1987
Caligo memnon memnon (= *Caligo telamonius memnon*)	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	Auerbach and Strong 1981, Santos and Benítez-Malvido in press
Caligo oileus scamander	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	De Vries 1987
Caligo teucer	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	Souza et al. 2006
Caligo Uranus	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	Santos and Benítez-Malvido in press
Caligo illioneus illioneus	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	Assis et al. 2002, Watanabe 2007, Specht and Paluch 2009
Castnia licus	Castniidae	Insecta	Rhizome and pseudostem	Pseudostem and rhizome boring	Generalist	Yes	Assis et al. 2002
Cephaloleia consanguinea	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Strong 1977a, b; Auerbach and Strong 1981, Strong 1982; McCoy 1984, 1985
Cephaloleia curtispatha	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Strong 1977a, b; Strong 1982
Cephaloleia instabilis	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Strong 1977a, b; Strong 1982
Cephaloleia neglecta	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Seifert and Seifert 1979
Cephaloleia nigripicta	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Strong 1977b, Strong 1982
Cephaloleia ornatrix	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Strong 1977a, b; Strong 1982

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Cephaloleia puncticollis	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Strong 1977a, b; Strong 1982
Cephaloleia sp. nov.	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Strong 1977a
Cephaloleia sp.1 (*belti complex*)	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Santos and Benítez-Malvido in press
Cephaloleia sp.2 (*instabilis-stenosoma complex*)	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Santos and Benítez-Malvido in press
Cephaloleia sp.3 (*instabilis-stenosoma complex*)	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Santos and Benítez-Malvido in press
Cephaloleia vicina	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	Strong 1977b, Strong 1982
Cephaloleia spp.	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	McKenna & Farrell 2005
Cheirispa dorsata	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Zingiberales	No	McCoy 1984, 1985
Chelobasis bicolor	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Heliconiaceae	No	Strong 1977a, b; Strong 1982
Chelobasis perplexa	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Heliconiaceae	No	Strong 1977a, b; Auerbach and Strong 1981, Strong 1982
Cornops frenatum frenatum	Acrididae	Insecta	Leaves	Unknown	Unknown	No	Braga et al. 2007
Dysmicoccus brevipes	Pseudococcidae	Insecta	Vascular tissue	Sap depletion	Generalist	Yes	Assis et al. 2002
Leptoscelis tricolor	Coreidae	Insecta	Vascular tissue	Sap depletion	Specialist on Heliconiaceae	Unknown	Miller and Hollander 2010
Mahanarva costaricensis	Cercopidae	Insecta	Vascular tissue	Sap depletion	Unknown	Yes	Peck et al. 2004

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Megalopyge sp.	Megalopygidae	Insecta	Leaves	Defoliation	Generalist	No	Auerbach and Strong 1981
Metraga sp.	Limacodidae	Insecta	Leaves	Defoliation	Generalist	No	Auerbach and Strong 1981
Nympharescus separutus	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Heliconiaceae	No	Strong 1977a, b; Strong 1982
Opsiphanes invirae	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	Assis et al. 2002
Opsiphanes tamarindi tamarindi	Nymphalidae	Insecta	Leaves	Defoliation	Specialist on Zingiberales	Yes	Auerbach and Strong 1981, De Vries 1987, Santos and Benítez-Malvido in press
Pentalonia nigronervosa	Aphididae	Insecta	Vascular tissue	Sap depletion	Generalist	Yes	Assis et al. 2002
Raoiella indica	Tenuipalpidae	Arachnidae	Leaves	Leaf spot	Specialist on Zingiberales	Yes	Peña et al. 2006, Torre-Santana et al. 2010
Sinervus baerensprungi	Miridae	Insecta	Vascular tissue	Sap depletion	Unknown	Yes	Ferreira et al. 2001
Spartacus albatus	Miridae	Insecta	Vascular tissue	Sap depletion	Unknown	Yes	Ferreira et al. 2001
Spartacus discovittatus	Miridae	Insecta	Vascular tissue	Sap depletion	Unknown	Yes	Ferreira et al. 2001
Spartacus minensis	Miridae	Insecta	Vascular tissue	Sap depletion	Unknown	Yes	Ferreira et al. 2001
Tarchon felderi	Apatelodidae	Insecta	Leaves	Defoliation	Generalist	No	Santos and Benítez-Malvido in press
Tetranychus abacae	Tetranychidae	Arachnidae	Leaves	Leaf spot	Generalist	Yes	Assis et al. 2002
Thyroptera tricolor	Thyropteridae	Chiroptera	Leaves	Leaf roosting	Specialist on Zingiberales, possibly	No	Vonhof et al. 2004

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Unknown Rodentia	Geomyidae	Mammalia	Roots, rhizome and pseudostem	Wilt and death	Unknown, possibly specialist on Zingiberales	Yes	B. A. Santos, pers. observ.
Unknown Homoptera	Unknown	Insecta	Vascular tissue	Sap depletion	Unknown	Unknown	Seifert 1982
Xenarescus monocerus	Chrysomelidae	Insecta	Leaves	Leaf scrapping	Specialist on Heliconiaceae	No	Strong 1977a, b; Seifert and Seifert 1979
Pathogens							
Acremonium sp.	Incertae sedis	Sordariomycetes	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995
Alternaria alternata	Pleosporaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Madriz et al. 1991, Costa 2007
Alternaria sp.	Pleosporaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Connelly 1999, Costa 2007, Santana et al. 2009a
Anthostomella minor	Xylariaceae	Sordariomycetes	Unknown	Unknown	Generalist	Yes	Farr and Rossman 2010
Anthostomella palmicola	Xylariaceae	Sordariomycetes	Unknown	Unknown	Generalist	Yes	Farr and Rossman 2010
Ascochyta sp.	Incertae sedis	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Costa 2007, Farr and Rossman 2010
Bipolaris buchloes	Pleosporaceae	Dothideomycetes	Leaves and inflorescences	Leaf and inflorescence spots	Generalist	Yes	Costa 2007
Bipolaris cynodontis	Pleosporaceae	Dothideomycetes	Leaves and inflorescences	Leaf and inflorescence spots	Generalist	Yes	Assis et al. 2002, Costa 2007, Santana et al. 2009b

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Bipolaris incurvata	Pleosporaceae	Dothideomycetes	Leaves and inflorescences	Leaf and inflorescence spots	Generalist	Yes	Sewake and Uchida 1995, Connelly 1999, Lins and Coelho 2004
Bipolaris setariae	Pleosporaceae	Dothideomycetes	Leaves and inflorescences	Leaf and inflorescence spots	Generalist	Yes	Assis et al. 2002, Costa 2007
Bipolaris sp.	Pleosporaceae	Dothideomycetes	Leaves and inflorescences	Leaf and inflorescence spots	Generalist	Yes	Sewake and Uchida 1995, Connelly 1999, Costa 2007, Farr and Rossman 2010
Bipolaris tripogonis	Pleosporaceae	Dothideomycetes	Leaves and inflorescences	Leaf and inflorescence spots	Generalist	Yes	Costa 2007
Calonectria spathiphylli	Nectriaceae	Sordariomycetes	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995, Farr and Rossman 2010
Cercospora heliconiae	Mycosphaerellaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Heliconiaceae	Yes	Farr and Rossman 2010
Cercospora sp.	Mycosphaerellaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995, Assis et al. 2002, Farr and Rossman 2010
Cerotelium rectangulata (= *Physopella rectangulata*)	Phakopsoraceae	Pucciniomycetes	Leaves	Rust	Specialist on Zingiberales	Yes	Hennen et al. 2005, Farr and Rossman 2010
Cladosporium herbarum	Davidiellaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Assis et al. 2002
Cladosporium sp.	Davidiellaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Farr and Rossman 2010
Coccomyces annulatus	Rhytismataceae	Leotiomycetes	Leaves	Leaf spot	Specialist on Zingiberales	Yes	Farr and Rossman 2010

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Cochliobolus heliconiae	Pleosporaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Heliconiaceae, possibly	Unknown	Alcorn 1996
Colletotrichum gloeosporioides (*Glomerella cingulata*)	Glomerellaceae	Sordariomycetes	Leaves and inflorescences	Anthracnose	Generalist	Yes	Madriz et al. 1991, Assis et al. 2002, Lins and Coelho 2004, Farr and Rossman 2010
Colletotrichum musae (= *Gloeosporium musarum*)	Glomerellaceae	Sordariomycetes	Leaves and inflorescences	Anthracnose	Generalist	Yes	Madriz et al. 1991
Colletotrichum sp.	Glomerellaceae	Sordariomycetes	Leaves and inflorescences	Anthracnose	Generalist	Yes	Sewake and Uchida 1995, Costa 2007
Corticium koleroga (= *Pellicularia koleroga*)	Corticiaceae	Agaricomycetes	All plant organs	Wilt and death	Generalist	Yes	Farr and Rossman 2010
Corynespora cassiicola	Corynesporascaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Farr and Rossman 2010
Corynespora elaeidicola	Corynesporascaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Farr and Rossman 2010
Curvularia brachyspora	Pleosporaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Assis et al. 2002
Curvularia lunata	Pleosporaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Lins and Coelho 2004, Costa 2007
Curvularia sp.	Pleosporaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Madriz et al. 1991, Farr and Rossman 2010
Cylindrocladium floridanum	Nectriaceae	Sordariomycetes	Leaves and rhizome	Leaf spot and rhizome rot	Generalist	Yes	Connelly 1999
Cylindrocladium sp.	Nectriaceae	Sordariomycetes	Leaves	Leaf spot	Generalist	Yes	Farr and Rossman 2010

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Cylindrocladium spathiphylli	Nectriaceae	Sordariomycetes	Leaves	Leaf spot	Generalist	Yes	Assis et al. 2002, Risède and Simoneau 2004
Deightoniella torulosa	Mycosphaerellaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Zingiberales	Yes	Farr and Rossman 2010
Drechslera musae-sapientum	Pleosporaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Zingiberales	Yes	Madriz et al. 1991, Farr and Rossman 2010
Eudarluca sp.	Phaeosphaeriaceae	Dothideomycetes	Unknown	Unknown	Generalist	Yes	Farr and Rossman 2010
Exserohilum rostratum	Pleosporaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995, Farr and Rossman 2010
Fusarium incarnatum (= *Fusarium semitectum*)	Nectriaceae	Sordariomycetes	All plant organs	Wilt and death	Generalist	Yes	Farr and Rossman 2010
Fusarium oxysporum	Nectriaceae	Sordariomycetes	All plant organs	Wilt and death	Generalist	Yes	Madriz et al. 1991, Connelly 1999, Assis et al. 2002, Lins and Coelho 2004
Fusarium sp.	Nectriaceae	Sordariomycetes	All plant organs	Wilt and death	Generalist	Yes	Sewake and Uchida 1995, Costa 2007, Farr and Rossman 2010
Guignardia heliconiae	Botryosphaeriaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Heliconiaceae	Yes	Farr and Rossman 2010
Guignardia musae	Botryosphaeriaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Zingiberales	Yes	Madriz et al. 1991
Hansfordia ovalispora	Incertae sedis	Incertae sedis	Unknown	Unknown, possibly leaf spot	Generalist	Yes	Farr and Rossman 2010
Helicotylenchus sp.	Hoplolaimidae	Secernentea	Roots	Root gall and shoot	Generalist	Yes	Lins and Coelho 2004

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
				wilt			
Helminthosporium sp.	Massarinaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Farr and Rossman 2010
Hendersonia sp.	Phaeosphaeriaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Farr and Rossman 2010
Heptaster hughesii	Incertae sedis	Dothideomycetes	Unknown	Unknown	Generalist	Unknown	Farr and Rossman 2010
Leptosphaeria coniothyrium (= *Coniothyrium fuckelii*)	Leptosphaeriaceae	Dothideomycetes	Unknown	Unknown, possibly anthracnose	Generalist	Yes	Farr and Rossman 2010
Macrophomina phaseolina	Botryosphaeriaceae	Dothideomycetes	All plant organs	Leaf spot and damping-off	Generalist	Yes	Farr and Rossman 2010
Mahabalella sp.	Incertae sedis	Incertae sedis	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995
Maravalia sp.	Chaconiaceae	Pucciniomycetes	Leaves	Rust	Unknown	Yes	Farr and Rossman 2010
Meliola heliconiae	Meliolaceae	Dothideomycetes	Unknown	Unknwon	Specialist on Heliconiaceae, possibly	Yes	Farr and Rossman 2010
Meliola macrospora	Meliolaceae	Dothideomycetes	Unknown	Unknwon	Unknown	Yes	Farr and Rossman 2010
Meliola musae	Meliolaceae	Dothideomycetes	Unknown	Unknwon	Specialist on Zingiberales	Yes	Farr and Rossman 2010
Meloidogyne incognita	Heteroderidae	Secernentea	Roots	Root gall and shoot wilt	Generalist	Yes	Lins and Coelho 2004
Meloidogyne sp.	Heteroderidae	Secernentea	Roots	Root gall and shoot wilt	Generalist	Yes	Connelly 1999

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Metasphaeria heliconiae	Dothioraceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Heliconiaceae, possibly	Yes	Farr and Rossman 2010
Metulocladosporiella musae (= *Cladosporium musae*)	Davidiellaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Zingiberales	Yes	Costa 2007
Musicillium theobromae (= *Verticillium theobromae*)	Plectosphaerellaceae	Sordariomycetes	Unknown	Unknown, possibly shoot rot	Generalist	Yes	Farr and Rossman 2010
Mycosphaerella musicola	Mycosphaerellaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Zingiberales	Yes	Madriz et al. 1991
Mycosphaerella sp.	Mycosphaerellaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Farr and Rossman 2010
Myrothecium cinctum	Incertae sedis	Sordariomycetes	Unknown	Unknwon, possibly rhizome rot	Generalist	Yes	Farr and Rossman 2010
Myrothecium renaudii	Incertae sedis	Sordariomycetes	Unknown	Unknwon, possibly rhizome rot	Unknown	Yes	Farr and Rossman 2010
Nectria heliconiae (= *Nectria subfalcata*)	Nectriaceae	Sordariomycetes	Unknown	Unknown, possibly wilt	Generalist	Yes	Farr and Rossman 2010
Nigrospora oryzae (= *Nigropora khuski oryzae*)	Incertae sedis	Sordariomycetes	Leaves	Leaf spot	Generalist	Yes	Costa 2007
Oidium sp.	Erysiphaceae	Leotiomycetes	Leaves	Powdery mildew	Generalist	Yes	Assis et al. 2002
Oxydothis grisea	Incertae sedis	Sordariomycetes	Unknown	Unknown	Generalist	Yes	Farr and Rossman 2010
Peltaster bertholletiae	Incertae sedis	Incertae sedis	Unknown	Unknown	Generalist	Yes	Farr and Rossman 2010
Periconia cookie	Incertae sedis	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Costa 2007

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Peristomialis berkeleyi	Bionectriaceae	Sordariomycetes	Leaves	Leaf spot, possibly	Generalist	Yes	Farr and Rossman 2010
Pestalotiopsis pauciseta	Amphisphaeriaceae	Sordariomycetes	Leaves	Leaf spot	Generalist	Yes	Serra and Coelho 2007
Pestalotiopsis sp.	Amphisphaeriaceae	Sordariomycetes	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995, Madriz et al. 1991, Costa 2007, Farr and Rossman 2010
Phaeoisariopsis cercosporoides	Mycosphaerellaceae	Dothideomycetes	Unknown	Unknown	Unknown	Unknown	Farr and Rossman 2010
Phaeoseptoria musae	Phaeosphaeriaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Zingiberales	Yes	Farr and Rossman 2010
Phoma leveillei	Incertae sedis	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Costa 2007
Phoma tropica	Incertae sedis	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Costa 2007
Phomopsis sp.	Diaporthaceae	Sordariomycetes	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995, Farr and Rossman 2010
Phyllosticta dardanoi	Botryosphaeriaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Heliconiaceae, possibly	Yes	Costa 2007, Farr and Rossman 2010
Phyllosticta heliconiae	Botryosphaeriaceae	Dothideomycetes	Leaves	Leaf spot	Specialist on Heliconiaceae	Yes	Farr and Rossman 2010
Phyllosticta sp.	Botryosphaeriaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995
Phytophthora nicotianae	Peronosporaceae	Peronosporea	All plant organs	Wilt and death	Generalist	Yes	Sewake and Uchida 1995
Phytophthora sp.	Peronosporaceae	Peronosporea	All plant organs	Wilt and death	Generalist	Yes	Connelly 1999
Pilidium acerinum (= *Leptothyrium cylindricum*)	Incertae sedis	Leotiomycetes	Leaves	Leaf spot	Generalist	Yes	Farr and Rossman 2010
Proliferobasidium heliconiae	Brachybasidiaceae	Exobasidiomycetes	Unknown	Unknown	Specialist on Heliconiaceae	Yes	Farr and Rossman 2010

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Pseudocercospora sp.	Mycosphaerellaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Sewake and Uchida 1995
Pseudorhynchia polyrhyncha	Trichosphaeriaceae	Sordariomycetes	Unknown	Unknown	Unknown	Unknown	Farr and Rossman 2010
Puccinia heliconiae (= *Uredo heliconiae*)	Pucciniaceae	Pucciniomycetes	Leaves	Rust	Specialist on Heliconiaceae	Yes	Assis et al. 2002, Lins and Coelho 2004, Hennen et al. 2005, Farr and Rossman 2010
Pyriculariopsis sp.	Incertae sedis	Incertae sedis	Leaves	Leaf spot	Unknown	Yes	Sewake and Uchida 1995
Pythium myriotylum	Pythiaceae	Peronosporea	All plant organs	Wilt and death	Generalist	Yes	Connelly 1999
Pythium sp.	Pythiaceae	Peronosporea	All plant organs	Wilt and death	Generalist	Yes	Sewake and Uchida 1995, Farr and Rossman 2010
Ralstonia solanacearum (= *Pseudomonas solanacearum*)	Ralstoniaceae	Beta Proteobacteria	All plant organs	Wilt and death	Generalist	Yes	Akiew and Hyde 1993, Sewake and Uchida 1995, Assis et al. 2002, Lins and Coelho 2004, Wicker et al. 2007, Zoccoli et al. 2009
Rhizoctonia solani	Ceratobasidiaceae	Agaricomycetes	All plant organs	Wilt and death	Generalist	Yes	Sewake and Uchida 1995, Farr and Rossman 2010
Septobasidium sp.	Septobasidiaceae	Pucciniomycetes	Unknown	Unknown, possibly leaves	Generalist	Yes	Farr and Rossman 2010
Septoria sp.	Mycosphaerellaceae	Dothideomycetes	Leaves	Leaf spot	Generalist	Yes	Costa 2007, Farr and Rossman 2010
Solheimia costispora	Incertae sedis	Incertae sedis	Unknown	Unknown	Generalist	Yes	Farr and Rossman 2010
Sphaeromma mazosiae	Incertae sedis	Incertae sedis	Unknown	Unknown	Generalist	Yes	Farr and Rossman 2010

Species	**Family**	**Class**	**Plant part affected**	**Major type of damage**	**Range of hosts**	**Agricultural importance**	**Reference**
Stachylidium bicolor	Incertae sedis	Incertae sedis	Unknown	Unknown	Generalist	Yes	Farr and Rossman 2010
Terriera latiascus	Rhytismataceae	Leotiomycetes	Unknown	Unknown	Unknown	Unknown	Farr and Rossman 2010
Xiphinema sp.	Longidoridae	Secernentea	Roots	Root gall and shoot wilt	Generalist	Yes	Lins and Coelho 2004
Zygosporium oscheoides	Incertae sedis	Incertae sedis	Leaves	Leaf spot, possibly	Generalist	Yes	Farr and Rossman 2010

CAPITULO III

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Insect Herbivory and Leaf Disease in Natural and Human Disturbed Habitats: Lessons from Early-Successional *Heliconia* Herbs

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ABSTRACT

The interaction of plants with insect herbivores and fungal pathogens can affect community dynamics, but there is little information on how this antagonistic interaction may be altered in human-disturbed tropical systems. We examined whether the amount and quality of foliar damage on the pioneer herbs *Heliconia latispatha* and *Heliconia collinsiana* are distinct on road edges and secondary riparian vegetation compared with natural gaps in continuous forest (controls) in Mexico. We also investigated some physical and biological mechanisms that may jointly explain such differences. The overall insect damage in *H. latispatha* was similar between road edges and natural forest gaps (8.0% vs. 7.2% of leaf area). Damage by caterpillars, however, decreased from 4.2 percent in forest gaps to 0.5 percent on road edges, whereas damage by leaf-cutting ants increased from 0 to 5.8 percent. In secondary riparian vegetation, where none of the leaves sampled were attacked by ants, overall herbivore damage in *H. collinsiana* was less than half that observed in forest gaps (3.0% vs. 6.7%), and driven mainly by differences in caterpillar damage (2.5% vs. 6.2%). By contrast, attack by leaf fungal pathogens was two to three times greater in both human-disturbed habitats than in gaps (8.2–9.6% vs. 3.7–4.2%). Potential mechanisms underlying these differences involved human-induced shifts in air and soil temperature driven by greater light availability, as well as changes in relative humidity, leaf toughness, foliar condensed tannins, and local abundance of herbivores. Our results indicate that human disturbance alters insect herbivory and may increase proliferation of leaf disease.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp.

Key words: biotic interaction; forest disturbance; pathogens; rain forest; riparian corridor; road effect.

The canopy of tropical rain forests is continuously changing as trees recruit into it and eventually fall due to windstorms, senescence, and lightning (Whitmore 1989). Treefall gaps help to maintain local species diversity in tropical rain forests by creating microenvironmental conditions that allow the growth and reproduction of species that cannot complete their life cycle under the shady conditions of old-growth forests (Brokaw 1985, Schnitzer & Carson 2001). Large-scale human disturbance of tropical rain forests is qualitatively and quantitatively different in its effects (Laurance & Bierregaard 1997, Cuarón 2000, Laurance & Peres 2006). While agriculture and cattle farming are among the major drivers of the current biodiversity crisis, other human actions such as the opening of roads (unpaved or not) can also have important ecological effects on natural ecosystems (Laurance *et al*. 2009). Road openings change vegetation structure, act as dispersal routes for some organisms (*e.g.*, invasive species) and as barriers for others, and also promote further human colonization and hunting (Laurance *et al*. 2009).

Current research on human-modified landscapes has mostly focused on forest remnants, with particular attention to edge and area effects (Malcolm 1994, Murcia 1995, Laurance *et al*. 2002, Harper *et al*. 2005). It is increasingly recognized, however, that the secondary vegetation that regenerates in the matrix abutting forest remnants is critical for biodiversity conservation in human-dominated tropical rain forest landscapes (Food and Agriculture Organization of The United Nations 2009, Gardner *et al*. 2009). These novel forests are expected to protect soils, cycle nutrients, support wildlife, store carbon, maintain watershed function, and possibly mitigate species extinction (Lugo 2009), but our understanding about their ecology is still in its infancy. A major question is to what extent key biotic interactions are altered in these increasingly common secondary forests (Laurance 2005).

Among the most common interactions in tropical forests are those between plants, insect herbivores, and leaf fungal pathogens (Gilbert & Hubbell 1996; García-Guzmán & Dirzo 2001, 2004; Benítez-Malvido & Lemus-Albor 2005, 2006). Folivorous insects and leaf fungal pathogens may reduce growth, survival, and reproductive success of their hosts, alter plant population structure, and influence successional pathways (see reviews by Coley & Barone 1996, Gilbert 2002, Marquis 2005, Burdon *et al*. 2006 and references therein). Plant-herbivore and plant-pathogen interactions should be altered in human-disturbed habitats for at least three reasons. First, microclimatic conditions tend to be unsuitable for many organisms and physical factors drive fungal disease development and transmission (Agrios 2005). In addition, shifts in microclimate may prevent insect eggs from hatching, alter physical and chemical characteristics of the leaves, and favor the proliferation of pioneer plant species that are poorly defended against herbivores (Coley & Barone 1996, Laurance *et al*. 2002). Second, isolation in space may prevent dispersal and colonization to new areas by many plants, insects, and fungi (Burdon 1993, Fáveri *et al*. 2008). Finally, human disturbance is usually more diverse, frequent, intense, and lasting in secondary forests than in primary forest, which impedes forest recovery and may disrupt plant-herbivore and plant-pathogen interactions (Uhl 1982, Benítez-Malvido & Lemus-Albor 2006).

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In this study, we focused on the folivorous insects and leaf fungal pathogens that attack the foliage of two early-successional perennial herbs of the genus *Heliconia* (Heliconiaceae), *H. latispatha* and *H. collinsiana*, which thrive in high light environments of forest gaps and human-disturbed Neotropical areas (Stiles 1975, Berry & Kress 1991). Our aim was to investigate whether the amount and quality of biotic damage on the foliage of *H. latispatha* and *H. collinsiana* are distinct on road edges and in secondary riparian vegetation compared with natural gaps in continuous forest and, if so, whether this is due to changes in microclimatic conditions (*i.e.*, air and soil temperature, air relative humidity, and light incidence), host availability and quality (*i.e.*, shoot density, leaf toughness, and foliar condensed tannins), and/or local abundance of key folivorous insects (*i.e.,* hispine beetles and caterpillars).

METHODS

Study area.—We conducted this study in the Montes Azules Biosphere Reserve (REBIMA in Spanish), state of Chiapas, southern Mexico, and the adjacent communal lands of the Ejido Chajul (16°08′ N, 90°55′ W). The REBIMA, created in 1978, is 330,000-ha in area and constitutes the main remnant of the Mesoamerican biodiversity hotspot (Myers *et al*. 2000, Figueroa *et al*. 2009). The primary vegetation type is lowland tropical rain forest, attaining 40 m in canopy height in alluvial terraces along main rivers (Siebe *et al*. 1995). Maximum and minimum annual temperatures are 31.8°C (April–May) and 18°C (January–February), respectively. Annual precipitation averages 3000 mm, with < 60 mm/mo from February through April, and more than 200 mm/mo from May to October (Benítez-Malvido & Lemus-Albor 2005). The REBIMA is bounded to its south by the Lacantún River, a 100–200 m wide watercourse that separate REBIMA's vast tracts of pristine old-growth forests from the severely fragmented landscape in which the Ejido Chajul is embedded. Forest conversion to cattle pastures and croplands in the region started in the mid-1970 s. Today, a mosaic of small forest fragments, secondary vegetation, human settlements, croplands, pastures, and roads composes the landscape.

For this study, we selected three habitat types in an early-successional stage ($<$ 5-yr old): (1) road edge, (2) secondary riparian vegetation, and (3) forest gap (Fig. S1). Road edge constituted a 5-km section of the Fronteriza freeway edges ($<$ 20 m from the road) and its paved access to the Ejido Chajul. Road edges were 3–6 km away from the nearest primary continuous forest; they were mostly surrounded by pastures and asphalt and dominated by early-successional shrubs and herbs (no arboreal vegetation), including *H. latispatha*. Secondary riparian vegetation represented a 4-km section of narrow ($<$ 50 m wide) secondary riparian corridors along the human-modified margin of the Lacantún River (in front of the REBIMA). It was surrounded by a mix of subsistence croplands and water and characterized by a discontinuous canopy of pioneer trees (*e.g.*, *Ficus* spp., *Cecropia* spp.). *Heliconia collinsiana* was particularly abundant in the open areas of these altered riparian zones. Forest gaps were represented by 19 large ($>$ 100 m^2), naturally formed young gaps embedded in a 3.5 km^2 area of the REBIMA, which were used as experimental controls. Thus, *H. latispatha* was sampled in forest gaps and on road edges and *H. collinsiana* was sampled in forest gaps and riparian vegetation. Road edges and secondary riparian vegetation are referred in the text as human-disturbed habitats, and forest gaps as natural-disturbed habitats.

Natural enemies.—There are three major groups of insects that attack mature and immature leaves of *Heliconia* in the Neotropics: hispine beetles, caterpillars, and leaf-cutting ants. Our field experience with the eight *Heliconia* species in the region of Chajul (Santos *et al*. 2009) confirmed that many species of these three major groups of insects attack both *H. latispatha* and *H. collinsiana* (Table S1). Hispine beetles are small chrysomelids (*ca* 1–2 cm in length) that feed exclusively on Zingiberales; those of the Arescini tribe (four genera) are specialist on Heliconiaceae, while those of the Cephaloliini tribe also feed on other Zingiberales families (Strong 1977a). Larvae feed from the surface of the host plant by dragging the mandibles reciprocally across the leaf surface while crawling slowly forward, leaving a feeding scar and a trail of frass (Strong 1977b, Wilf *et al*. 2000). The mechanics of feeding is similar for adults; often adult feeding produces small ellipsoid holes at the margin of the rolled young leaves (Strong 1977b).

The caterpillar species that attack the foliage of *Heliconia* vary in body size and diet breadth. The most common and specialized are those of the genera *Caligo* and *Opsiphanes* (Nymphalidae), which are among the largest caterpillars of the Neotropics (up to 20 cm in length) (De Vries 1987). These 'giant' caterpillars feed mostly on Heliconiaceae and Musaceae, and to a limited extent, on Marantaceae, Arecaceae, and Cylanthaceae (De Vries 1987, Watanabe 2007). Smaller, more generalist caterpillars such as *Antichloris eriphia* (Arctiidae), *Tarchon felderi* (Apatelodidae), and *Sibine apicalis* (Limacodidae) also have been recorded feeding on *Heliconia* leaves (Auerbach & Strong 1981, Assis *et al.* 2002, B. A. Santos, pers. obs.). In initial instars, the small mouthparts of larvae allow them to only scrape the underside of the leaf (Auerbach & Strong 1981, Assis *et al.* 2002). As they grow up, however, they cause defoliation either from the edge to the center of the leaf (*e.g.*, *Caligo* or *Opsiphanes* damage) or throughout the leaf blade, leaving elongated holes usually perpendicular to the leaf central vein (*e.g.*, *Antichloris* damage) (Assis *et al.* 2002).

Leaf-cutting ants belonging to the tribe Attini are among the most important generalist insect herbivore in the Neotropics (Rico-Gray & Oliveira 2007). They cut leaves of monocots and dicots from the edge to the center of the leaf, always in a half-moon shape, causing total defoliation in some cases (Assis *et al*. 2002). Because each insect group produces characteristic feeding marks, we could estimate the relative damage caused by each of them with high certainty. This procedure, however, cannot be repeated with the leaf fungal pathogens because infection by different pathogens may cause similar symptoms (see Sewake & Uchida 1995, Assis *et al.* 2002, Lins & Coelho 2004, Hennen *et al*. 2005, Serra & Coelho 2007 for a list of major pathogens attacking *Heliconia* and the symptoms they cause). Pathogen damage was indicated by leaf spots or 'blotching' that varied in size, color, and shape.

Standing levels of biotic damage.—To estimate the standing levels of foliar damage associated with leaf herbivores and pathogens of *H. latispatha* and *H. collinsiana*, in December 2008 we randomly sampled ten clumps of *H. latispatha* along road edges, ten clumps of *H. collinsiana* in secondary riparian vegetation, and ten clumps of each species in forest gaps (clumps are a group of shoots that sprout from the same rhizome). In all habitats, sampled clumps were at least 50 m away from the nearest conspecific clump; *H. latispatha* and *H. collinsiana* co-occurred in only one of the 19 forest gaps sampled. To control for differences in clump size across habitats, only small clumps (3–10 shoots) were examined.

We randomly collected and photographed ten fully expanded leaves from each clump using a 10-megapixel digital camera (Nikon Coolpix P80) and a blue background panel. Photographs were taken with a macro lens (maximum focal length 84.2 mm) when leaves were flattened on the blue panel to avoid distortion. They were further processed using the image analysis software ASSESS (Lamari 2002) to quantify total leaf area and estimate the percentage of leaf area damaged by hispine beetles, caterpillars, leaf-cutting ants, unknown herbivores, and leaf-fungal pathogens. A 2.5 cm × 2.5 cm scale was affixed to the blue panel for image calibration and the subsequent leaf area quantification. We used percentage of leaf area damaged as a response variable instead of the absolute leaf area damaged because mean leaf area was smaller in human-altered habitats (Table S2). We averaged foliar attack and damage levels of shoots per clump for the purposes of the analyses.

Microclimatic conditions.—To characterize the microclimate along road edges and in secondary riparian vegetation and forest gaps, we installed two HOBO© data loggers model U12 per habitat type in zones where the two study species of *Heliconia* were present. The location of the data loggers was determined by randomly selecting two of the ten replicates (clumps) of each habitat. Data loggers were positioned at 1.3 m above the ground and set to record hourly measures of air temperature, air relative humidity, light incidence, and soil temperature (at 5 cm depth). Microclimatic data recording started on 27 September 2009 at 1000 h and ended 5 d later on 2 October 2009 at 0900 h, resulting in 120 observations per microclimatic variable per site. According to the HOBO manual, accuracy of measurements is $\pm 0.35^{\circ}$C for temperature and ± 2.5 percent for relative humidity (up to 80% of relative humidity); accuracy is not provided by the manufacturer for light measurements in outdoor conditions, however.

Host availability and quality.—We assessed host-plant availability in December 2008 by counting the number of conspecific shoots in a 10-m radius from clumps sampled for standing levels of biotic damage. In September 2009, a 20 cm × 10 cm segment of three undamaged, fully expanded leaves (second, third, and fourth leaf) was collected from ten same-aged, nonreproducing shoots in each habitat type (one shoot per clump). Leaf segments without the leaf central vein were then processed in laboratory to quantify the absorbance of condensed tannins following Waterman and Mole (1994); absorbance was read in the spectrophotometer Thermo© Genesis 20 at 550 nm wavelength. Although absorbance does not provide a precise measure of tannin concentration, it gives a readily comparable index of the amount of tannins in our samples (Fáveri *et al.* 2008). We used a 3-mm diameter rod to measure leaf toughness as the force necessary to perforate the leaf blade (Boege 2005; force was expressed in g/cm^2). We perforated the middle section of ten fully expanded leaves randomly selected from ten small clumps of each species in each habitat (10 leaves per clump). All chemical and physical foliar characteristics were averaged per clump for the purposes of the analyses.

Herbivore abundance.—To assess if anthropogenic disturbance alters the local abundance of folivorous insects associated with *Heliconia*, in September 2009 we randomly selected another set of ten clumps of *H. latispatha* along road edges, ten clumps of *H. collinsiana* in secondary riparian vegetation and ten clumps of each species in forest gaps. We collected all chrysomelids (larvae and adults) and caterpillars found on *Heliconia* shoots: including the pseudostem, leaf blade, petiole, and inflorescence when present. Insects were placed in plastic pots containing alcohol (70%) and subsequently identified to the lowest possible taxonomic level.

Statistical analyses.—For each *Heliconia* species separately, we used a split-plot analysis of variance (ANOVA) to compare the levels of herbivory by distinct insect groups between habitats. The split-plot ANOVAs had habitat type set as the whole-plot factor, insect group as the subplot factor, and clump as the blocking variable (Potvin 2001). There were two levels of the whole-plot factor (road edges and forest gap for *H. latispatha* and riparian vegetation and forest gap for *H. collinsiana*), four levels of the subplot factor 'insect group' in the *H. latispatha* model (hispine beetles, caterpillars, leaf-cutting ants, and unknown herbivores), and only three in the *H. collinsiana* model (hispine beetles, caterpillars, and unknown herbivores), given that this species was not attacked by leaf-cutting ants (see 'Results'). One-way ANOVAs were used to test for differences in overall pathogen damage, density of conspecific shoots, absorbance of condensed tannins, leaf toughness, and local abundance of herbivores between habitats. Percentages of herbivore and pathogen damage were arcsine-square-root transformed and local abundance of herbivores and density of conspecific shoots were log-transformed (log $[x+1]$) before analyses.

We used generalized linear mixed models (GLMM) to test for differences in microclimate conditions among habitats. Habitat type (between-subject factor), hour of the day (within-subject factor), and their interaction was set as fixed effect and site (subject) was set as random effect (von Ende 2001). We adopted this procedure rather than other methods traditionally used to analyze repeated measures (*i.e.*, repeated-measure ANOVA, MANOVA, and profile analysis) because mixed models can handle many levels of the repeated measure factor and can be performed assuming different forms of the variance–covariance matrix (von Ende 2001). We ran GLMMs in JMP 7 (SAS Institute Inc.) using the restricted maximum likelihood method to separate the variance of fixed effects from that of the random effect. Relative humidity and light data were arcsine-square-root and log-transformed before analyses, respectively. All figures show untransformed data.

RESULTS

Standing levels of herbivore damage.—Herbivore attack was observed in 90 percent of *H. latispatha* leaves (95% in forest gaps and

84% on road edges). The most frequent damage was by hispine beetles (75% of the leaves), followed by caterpillars (21%), leaf-cutting ants (19%), and unknown herbivores (6%). Overall, insects removed similar percentages of leaf area in forest gaps (7.2% ± 1.0 %; mean ± SE) and road edges (8.0% ± 3.4%) ($F_{1,\,18} = 0.02$; $P = 0.884$). However, the relative damage owing to each insect group clearly depended on habitat type ($F_{3,\,54} = 11.13$; $P < 0.0001$). While caterpillars reduced their average damage from 4.2 percent in forest gaps to 0.5 percent on road edges, foliar attack by leaf-cutting ants increased from 0 to 5.8 percent (Fig. 1A). Hispine beetle damaged around 2.1 percent of leaf area irrespective of habitat type (Fig. 1A), indicating that attack by beetles was very common but did not cause much damage.

Similar to *H. latispatha*, herbivore attack was very common in the foliage of *H. collinsiana*, as 84 percent of the leaves showed some kind of insect damage (88% in forest gaps and 80% in secondary riparian vegetation). The most frequent damage was by hispine beetles (54% of the leaves), followed by caterpillars (46%), and unknown herbivores (28%). *Heliconia collinsiana* leaves were not attacked by leaf-cutting ants during our study. The overall herbivore damage was halved in secondary riparian vegetation compared with forest gaps (3.0% ± 1.1% vs. 6.7% ± 1.8%) ($F_{1,\,18} = 3.79$; $P = 0.067$). As observed in *H. latispatha*, the relative contribution of distinct herbivores varied with habitat type ($F_{2,\,36} = 3.56$; $P = 0.038$), especially because caterpillar damage decreased from 6.2 ± 1.8 percent in forest gaps to 2.5 ± 1.0 percent in secondary riparian vegetation (Fig. 1B).

STANDING LEVELS OF PATHOGEN DAMAGE.—Leaves of *H. latispatha* and *H. collinsiana* showed several necrotic lesions variable in color, form, and size. Most lesions were small, dark-brown, irregular, with a yellow halo measuring 1–2 mm; they coalesced in some leaves to form large necrotic areas, suggesting pathogenic fungi such as *Bipolaris*, *Cylindrocladium*, or *Cladosporium* as potential causal agents. *Cercospora* and *Puccinia*-like damage were also observed, as some leaves showed olive-green to brown lesions frequently clustering along veins, as well as oval chlorotic spots with reddish-brown centers on the adaxial leaf surface.

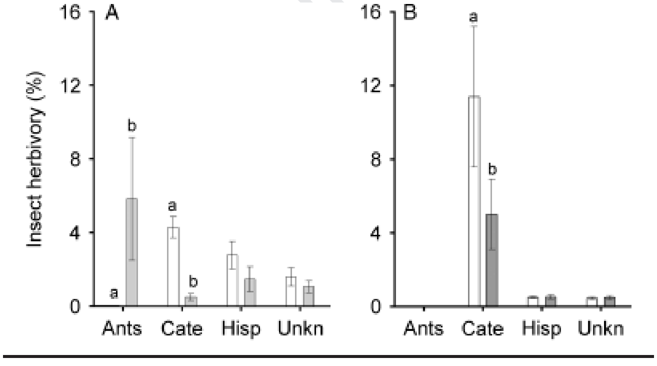

FIGURE 1. Standing levels of foliar damage (mean ± SE) by leaf-cutting ants (Ants), caterpillars (Cate), hispine beetles (Hisp), and unknown insects (Unkn) on the foliage of (A) *Heliconia latispatha* and (B) *Heliconia collinsiana* in forest gaps (white bars), road edges (lightly shaded bars), and secondary riparian vegetation (dark-shaded bars) in the region of Chajul, southern Mexico. Different letters indicate significant differences between habitats (Tukey–Kramer HSD test, $P < 0.05$).

About 65 percent of the *H. latispatha* leaves were damaged by pathogens (60% in forest gaps and 69% on road edges). Pathogen damage was associated with insect damage, as 91 percent of the infected leaves were concurrently attacked by herbivores (96% in forest gaps and 86% on road edges). There was great variation in the leaf area damaged by fungal pathogens among clumps (Fig. 2A). Also, on average, the percentage of leaf area infected was greater on road edges than in forest gaps (8.2% ± 2.4% vs. 4.2% ± 1.0%; Fig. 2A), but this difference was not statistically significant ($F_{1,\,19} = 1.89$; $P = 0.186$).

A similar trend was observed in the leaves of *H. collinsiana*. Most leaves (70%) showed symptoms of foliar disease (67% in forest gaps and 72% in secondary riparian vegetation), and 87 percent of the infected leaves were also damaged by insects (94% in forest gaps and 81% in secondary riparian vegetation). Likewise, disease severity was very variable among clumps and was greater in secondary riparian vegetation than in forest gaps (9.6% ± 4.1% vs. 3.7% ± 1.9%; Fig. 2B), though the effect of habitat type on pathogen damage was not significant ($F_{1,\,19} = 2.19$; $P = 0.156$).

MICROCLIMATIC CONDITIONS.—Daily patterns of microclimatic conditions were very similar between secondary riparian vegetation and forest gaps, but road edges clearly showed a different microclimate regime characterized by greater amplitudes of variation (Fig. 3). The differences among road edges and the other habitats depended on the hour of the day, as indicated by the significant effect of the *habitat* × *time* interaction in all analyzes (Table 1). The among-habitat disparity occurred mostly between 1000 h and 1800 h, when road edges showed higher air and soil temperature, higher light incidence, and lower air relative humidity, compared with forest gaps and secondary riparian vegetation. Road edges also had warmer soils over the night (Fig. 3).

HOST AVAILABILITY AND QUALITY.—The density of *H. latispatha* shoots was about fourfold greater on road edges than forest gaps

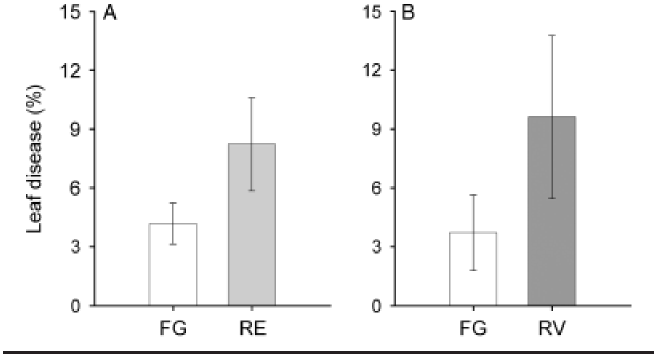

FIGURE 2. Standing levels of pathogen damage (mean ± SE) on the foliage of (A) *Heliconia latispatha* and (B) *Heliconia collinsiana* in forest gaps (FG), road edges (RE), and secondary riparian vegetation (RV) in the region of Chajul, southern Mexico.

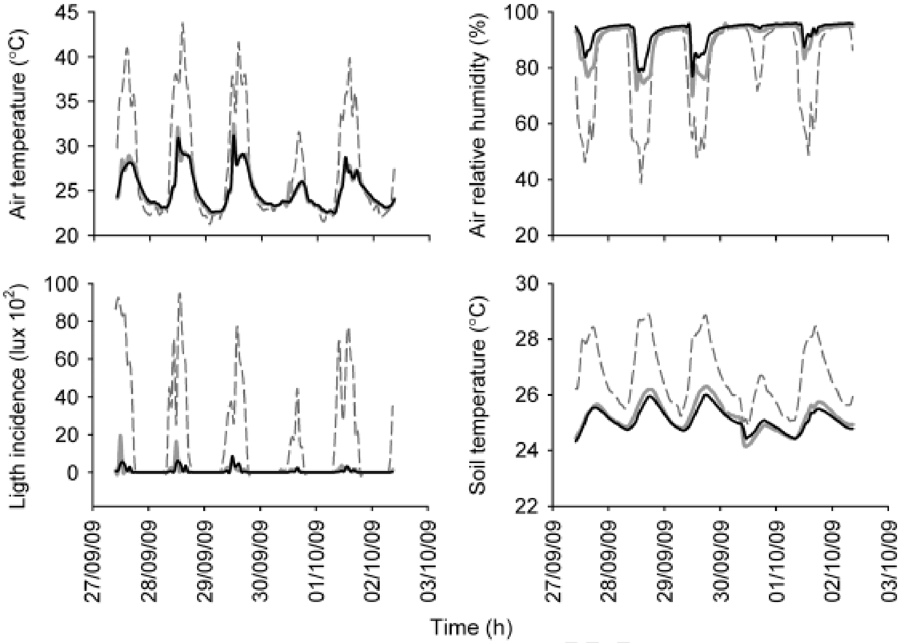

FIGURE 3. Daily patterns of air temperature, air relative humidity, light incidence, and soil temperature in forest gaps (black solid line), road edges (dashed line), secondary riparian vegetation (gray solid line) in the region of Chajul, southern Mexico. Recording started on 27 September 2009 at 1000 h and ended on 2 October 2009 at 0900 h. Each curve was constructed by averaging measures from two sites per habitat type.

($F_{1,18} = 8.49$; $P < 0.01$; Fig. 4A). Absorbance of condensed tannins in this species decreased by twofold on road edges when compared with forest edges ($F_{1,18} = 4.66$; $P = 0.045$; Fig. 4B). In contrast, leaf toughness increased by 50 percent on road edges ($F_{1,18} = 138.5$; $P < 0.0001$; Fig. 4C).

TABLE 1. *Fixed effects of generalized linear mixed models fitted for repeated measures of four microclimatic variables in the region of Chajul, Chiapas, and Mexico.*

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	2,3	4.52	0.124	0.90
Time	119,357	18.00	< 0.0001	
Habitat × time	238,357	3.30	< 0.0001	
Air relative humidity				
Habitat	2,3	8.47	0.058	0.93
Time	119,357	23.27	< 0.0001	
Habitat × time	238,357	4.48	< 0.0001	
Light incidence				
Habitat	2,3	13.02	0.033	0.94
Time	119,357	31.20	< 0.0001	
Habitat × time	238,357	3.56	< 0.0001	
Soil temperature				
Habitat	2,3	3.86	0.148	0.85
Time	119,357	5.13	< 0.0001	
Habitat × time	238,357	1.35	0.005	

The density of *H. collinsiana* shoots was tenfold greater in secondary riparian vegetation than in forest gaps ($F_{1,18} = 16.4$; $P < 0.001$; Fig. 4D). Absorbance of condensed tannins did not differ between habitats ($F_{1,18} = 0.14$; $P = 0.705$; Fig. 4E), whereas leaf toughness of *H. collinsiana* was on average 17 percent greater in secondary riparian vegetation than in forest edges ($F_{1,18} = 15.7$; $P < 0.001$; Fig. 4F).

HERBIVORE ABUNDANCE.—We collected a total of 73 individual herbivores on the foliage of *H. latispatha* (44 specimens in forest gaps and 29 on road edges). The abundance of hispine beetles did not differ between forest gaps and road edges ($F_{1,18} = 0.31$; $P = 0.585$; Fig. 5A), but the abundance of caterpillars was significantly reduced by sixfold along road edges (1.7 ± 0.6 vs. 0.3 ± 0.2 individuals per clump) ($F_{1,18} = 6.36$; $P = 0.021$; Fig. 5B).

A similar pattern was observed in *H. collinsiana*, where 54 herbivores were recorded (38 in forest gaps and 16 in secondary riparian vegetation). The abundance of chrysomelids did not differ between habitats ($F_{1,18} = 0.80$; $P = 0.382$; Fig. 5C), but the abundance of caterpillars was three times lower in secondary riparian vegetation than in forest gaps (2.7 ± 0.7 vs. 0.9 ± 0.3 individuals per clump) ($F_{1,18} = 4.72$; $P = 0.043$; Fig. 5D).

DISCUSSION

HABITAT DISTURBANCE AND BIOTIC DAMAGE.—Our results indicate that the interaction of early-successional *Heliconia* species with their folivorous insects is altered in human-disturbed areas of Southern Mexico. This alteration seems to be caused by a combined effect of

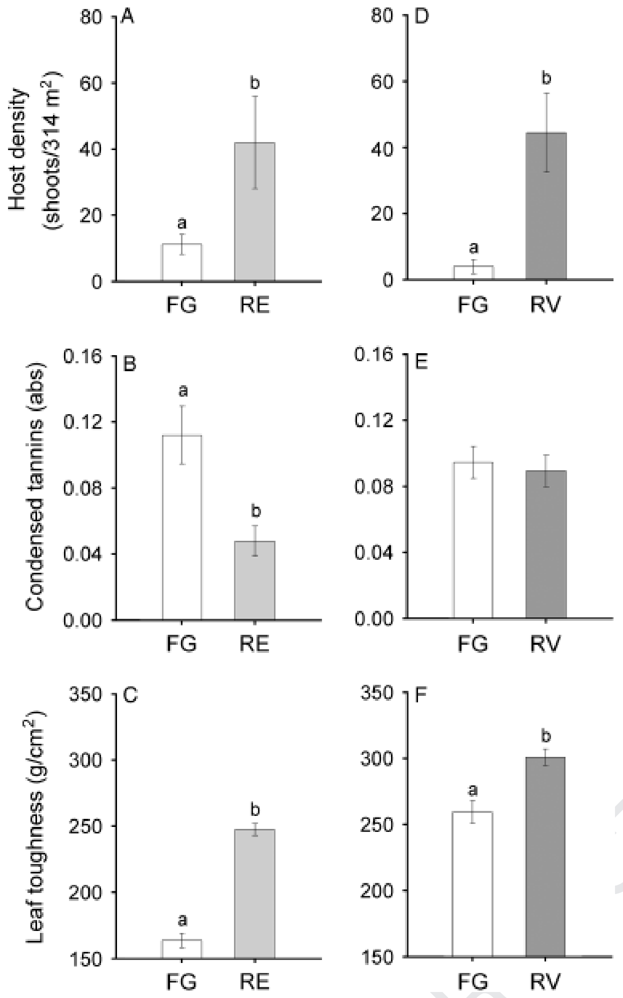

FIGURE 4. Host density, absorbance of foliar condensed tannins and leaf toughness (mean ± SE) of *Heliconia latispatha* (A–C) and *Heliconia collinsiana* (D–F) in forest gaps (FG), road edges (RE), and secondary riparian vegetation (RV) in the region of Chajul, southern Mexico. Different letters indicate significant differences between habitats (Tukey–Kramer HSD test, $P < 0.05$).

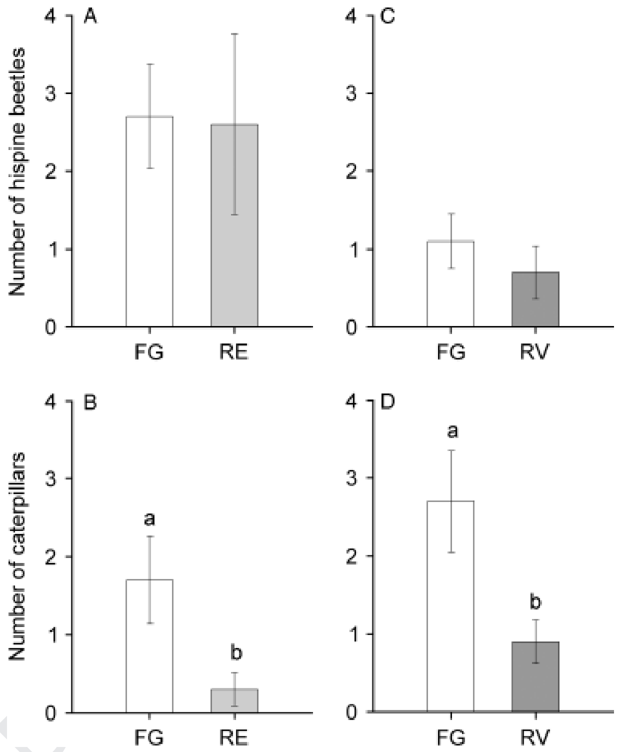

FIGURE 5. Local abundance of hispine beetles and caterpillars (mean ± SE) on the foliage of *Heliconia latispatha* (A–B) and *Heliconia collinsiana* (C–D) in forest gaps (FG), secondary riparian vegetation (RV), and road edges (RE) in the region of Chajul, southern Mexico. Different letters indicate significant differences between habitats (Tukey–Kramer HSD test, $P < 0.05$).

changes in microclimatic conditions, host availability, host quality, and local abundance of herbivores. Although we have quantified standing levels of damage instead of herbivory rates (rates are more appropriate to estimate herbivory because damaged leaves can lose tissue at different rates), some general patterns emerged from our findings. First, the total amount of leaf area removed from *Heliconia* in human-disturbed habitats depended mostly on the presence of leaf-cutting ants: when ants were present (road edge) they offset the reduction in caterpillar damage, leaving total levels of foliar damage similar between anthropogenically and naturally disturbed habitats. When they were absent (secondary riparian vegetation), the compensation did not occur, so herbivory levels diminished in human-disturbed areas.

The activity of leaf-cutting ants is known to increase with anthropogenic disturbance (Wirth *et al.* 2007, 2008). In fragmented forests their density may increase by 10–100-fold and remain elevated over time due to the continuous proliferation of pioneer tree species and local extirpation of predators and parasitoids (Terborgh *et al.* 2001, Almeida *et al.* 2008, Meyer *et al.* 2009). Positive responses of leaf-cutting ants to the creation of roads have been also reported. In the Brazilian Cerrado, where the number of colonization attempts is five to ten times greater on roads than in the adjacent vegetation, despite the elevated rates of foundress queen predation on roads (Vasconcelos *et al.* 2006). Because these insects are important agricultural pests (Rico-Gray & Oliveira 2007), they are removed from croplands by a variety of practices (from insecticides to fire). These abiotic pest control practices are currently used in our study area and may explain why leaf-cutting ants did not attack the palatable leaves of *H. collinsiana* in the secondary riparian vegetation, which was adjacent to many maize, bean, and chili crops (road edges were not).

The incidence of plant disease is expected to increase in human-modified landscapes due to at least four reasons (Benítez-Malvido & Lemus-Albor 2006). First, altered microclimatic conditions may favor certain pathogens and/or cause stress to plants that increase their susceptibility to disease. Second, poorly defended pioneer plants usually proliferate after anthropogenic disturbance, potentially increasing disease incidence at the community level. Third, exotic species, which become common in human-modified landscapes, may facilitate the introduction of novel pathogens. Finally, roads and vehicles may also serve as vectors for some exotic pathogens. Our results corroborate this general prediction by demonstrating that clumps of *Heliconia* in human-altered habitats tended to have a greater proportion of leaf area damaged by pathogens than those in natural disturbed habitat. This trend was consistent for the two species examined, although not statistically significant.

MICROCLIMATE AND BIOTIC DAMAGE.—Microclimatic shifts are one of the first consequences of human disturbance in tropical rain forests. Most of the information generated so far on microclimate has been used to describe edge effects in forest remnants (*e.g.*, Williams-Linera 1990, Camargo & Kapos 1995, Didham & Lawton 1999, Newmark 2001, Pohlman *et al.* 2007). Few studies have examined microclimatic conditions outside forest remnants despite their potential impact on species distribution and biotic interactions at the landscape level (Kapos *et al.* 1993, Williams-Linera *et al.* 1998). We observed significant microclimatic shifts on road edges, but not in narrow (< 50 m) secondary riparian corridors bordered by waterways and croplands. On one hand, this result indicates that a matrix of water may ameliorate harsh microclimatic conditions in disturbed landscapes, as do big trees scattered over a matrix of pastures (Williams-Linera *et al.* 1998). On the other hand, it emphasizes the strong negative edge effects of roads on microclimate (Delgado *et al.* 2007), especially when the road crosses highly deforested areas.

Our findings also indicate that shifts in microclimatic conditions *per se* are not enough to predict changes in the interaction of *Heliconia* with their insect herbivores in the region of Chajul. Host availability and local abundance of hispine beetles and caterpillars varied between habitats with either contrasting (road edge vs. forest gap) or similar microclimate (secondary riparian vegetation vs. forest gap), suggesting that there are other factors regulating the *Heliconia*–insect interaction in the region of Chajul. For instance, the greater density of *Heliconia* shoots on road edges and in riparian vegetation is more likely to be a result of past coppicing in these areas, which favor the production of new shoots (Berry & Kress 1991). The unexpected high tolerance of hispines to the drier and hotter conditions of road edges (eggs are very subject to desiccation [Strong 1977b]) may be a response to the greater availability of shoots and associated rolled leaves in this habitat, which provide suitable microhabitat for their growth and reproduction (Strong 1977a, b; Seifert 1982). Finally, the low abundance of caterpillars in the secondary riparian vegetation also suggests that the microclimate *per se* does not regulate the *Heliconia*–insect system. In fact, the reduction in caterpillar abundance in human-altered areas might be associated with either higher predation pressure (Dyer *et al.* 2005) and/or dispersal limitation (Fáveri *et al.* 2008) in these habitats.

HOST QUALITY AND BIOTIC DAMAGE.—Host quality may affect insect growth and fecundity and therefore influence plant–insect interactions (Awmack & Leather 2002). Our results indicate that *Heliconia* leaves in human-disturbed habitats became better defended physically but poorly defended chemically (especially *H. latispatha*). The increase in leaf toughness, which is likely the best defensive strategy in the genus *Heliconia* (Dominy *et al.* 2008; *Heliconia* appear to have few secondary compounds [Gage & Strong 1981]), might be a plausible explanation for the decrease in caterpillar damage we observed. The magnitude of the human-induced increase in leaf toughness (41–84 g/cm^2), however, was smaller than the difference naturally observed between the *Heliconia* species examined (96 g/cm^2), suggesting that caterpillars could overcome the alteration in leaf toughness originated by human disturbance as they overcome the difference among the species they feed on (there is no caterpillar specialized on only one *Heliconia* species; see De Vries 1987). Similarly, many hispine beetles can feed on *Heliconia* species that differ considerably in foliage quality (Strong 1977a, b; Auerbach & Strong 1981).

CONCLUSIONS

In sum, levels of insect herbivory in the foliage of *Heliconia* may be altered in human-disturbed habitats mostly due to changes in the abundance of herbivores (*i.e.*, proliferation of leaf-cutting ants and reduction in caterpillar abundance). Agricultural practices close to our study areas are likely to determine shoot availability and the presence of ant colonies in human-disturbed habitats, while potential higher predation pressure and/or dispersal limitation seem to limit local abundance of caterpillars in these habitats. The neutral response of hispines to human disturbance appears to be related to the higher availability of rolled leaves in human-altered habitats. While microclimate and host quality shifts are important, they are apparently not critical for the maintenance of the entire *Heliconia*–insect system in our study area. More attention should be paid to the disease ecology of novel forests because leaf fungal pathogens tend to cause more damage in human-disturbed habitats. Further studies with other plant growth forms (*e.g.*, trees and lianas) and their natural enemies (*e.g.*, seed predators, obligate pathogens) will help us better understand plant–herbivore and plant–pathogen interactions in the novel tropical forests that increasingly characterize most tropical landscapes.

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SUPPORTING INFORMATION

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

TABLE S1. Heliconia *herbivores recorded in forest edges, road edges and secondary riparian vegetation in the region of Chajul, southern Mexico.*

TABLE S2. *Structural and reproductive characteristics of 40* Heliconia *clumps sampled for standing levels of biotic damage in forest gaps, road edges, and secondary riparian vegetation in the region of Chajul, southern Mexico.*

FIGURE S1. Schematic diagram of the study area in Chajul, southern Mexico.

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TABLE S1. Heliconia *herbivores recorded in forest edges (FG), road edges (RE) and secondary riparian vegetation (RV) in the region of Chajul, Southern Mexico. Insect species were observed during the development of this study (from December 2008 to September 2009) on sampled and non-sampled clumps of H. latispatha and H. collinsiana.*

Insect group	**Family**	**Habitat type**		
		FG	**RE**	**RV**
Hispine beetle				
*Cephaloleia sp.*1 (belti complex)[a]	Chrysomelidae	X	X	X
*Cephaloleia sp.*2 (instabilis-stenosoma complex)[b]	Chrysomelidae	X	X	X
*Cephaloleia sp.*3 (instabilis-stenosoma complex)[b]	Chrysomelidae	X	X	X
Unknown 1	Chrysomelidae	X	X	X
Unknown 2	Chrysomelidae	X		X
Caterpillar				
Caligo uranus	Nymphalidae	X		
Caligo memnon	Nymphalidae	X		
Opsiphanes tamarindi tamarindi	Nymphalidae		X	X
Antichloris sp.	Arctiidae	X		X
Tarchon felderi	Apatelodidae	X		
Acharia cf. stimulea	Limacodidae	X	X	X
Leaf-cutting ant				
Atta cephalotes	Formicidae	X	X	X

[a] The belti complex contains 10 species scattered throughout Central America (C. Staines, pers. comm.)

[b] The instabilis-stenosoma complex has only two species which are extremely varibale in coloration (C. Staines, pers. comm.)

TABLE S2. *Structural and reproductive characteristics (mean ± SE) of 40* Heliconia *clumps sampled for standing levels of biotic damage in forest gaps (FG), road edges (RE), and secondary riparian vegetation (RV) in the region of Chajul, Southern Mexico. Ten clumps were sampled for each species in each habitat.*

Species	Habitat type		*F*-value	*P*-value
	Natural disturbed	Human disturbed [a]		
Heliconia latispatha				
Mean number of shoots	4.2 ± 0.5	4.5 ± 0.7	0.13	0.722
Mean number of leaves	11.9 ± 1.0	13.4 ± 1.8	0.54	0.470
Mean leaf area (cm^2)[b]	1380 ± 169	950 ± 114	4.42	<0.05
Mean shoot height (m)[c]	2.5 ± 0.2	1.6 ± 0.1	16.27	<0.001
No. of inflorescences	0.8 ± 0.2	0.8 ± 0.2	0	1.000
No. of flowers	62.5 ± 17.3	51.6 ± 15.5	0.22	0.645
Heliconia collinsiana				
Mean number of shoots	4.6 ± 0.5	4.9 ± 0.9	0.08	0.785
Mean number of leaves	15.4 ± 1.4	16.3 ± 2.4	0.10	0.752
Mean leaf area (cm^2)[b]	2752 ± 252	2014 ± 138	6.57	<0.05
Mean shoot height (m)[c]	3.2 ± 0.3	2.2 ± 0.1	10.62	<0.01
No. of inflorescences	0.4 ± 0.2	0.2 ± 0.1	0.60	0.449
No. of flowers	57.3 ± 32.8	41.6 ± 13.1	1.17	0.293

[a] Road edges for *H. latispatha* and secondary riparian vegetation for *H. collinsiana*

[b] Ten leaves were measured per clump

[c] Averaged from all shoots of the clump

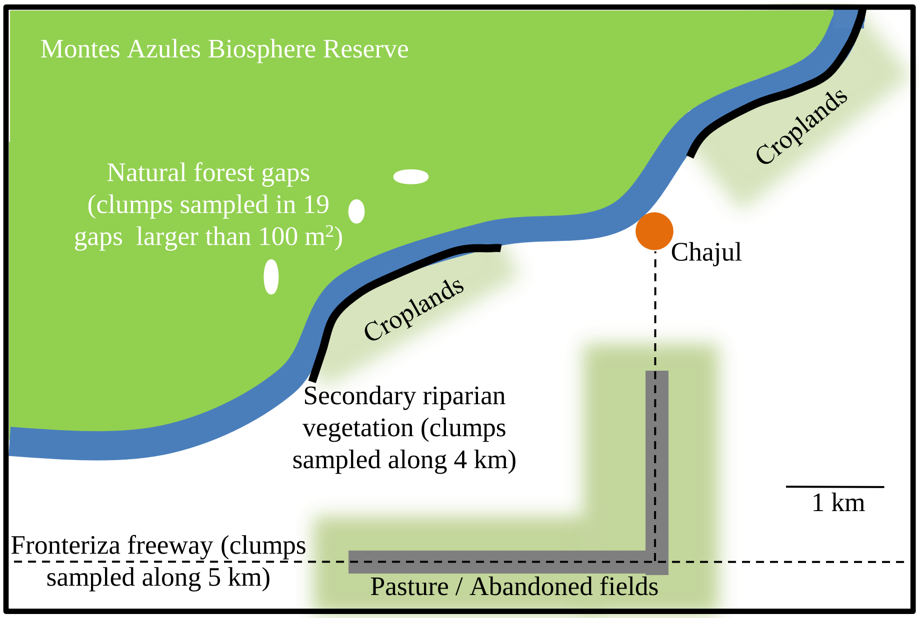

Figure S1. Schematic diagram of the study area in Chajul, Southern Mexico.

CAPITULO IV

LRH: Santos & Banítez-Malvido

RRH: Herbivory in forest fragments

Proliferation of leaf-cutting ants in forest fragments: an additional herbivory pressure or a functional compensation for locally extirpated specialist herbivores?

(Enviado a Biotropica)

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ABSTRACT

Generalist herbivores are becoming increasingly dominant in tropical forest fragments in detriment of specialist herbivores, but our understanding on how this shift affects plant populations is still very limited. We compared the amount of foliar damage owing to generalist and specialist insects on the understory herb *Heliconia aurantiaca* in forest fragments and continuous forests in Southern Mexico. We also assessed some physical and biological mechanisms underlying differences in foliar attack (*i.e.,* daily microclimatic patterns, host availability and quality) and quantified the effect of foliar damage on host growth, survival, and reproductive success over two years. The overall level of insect damage on *H. aurantiaca* was very similar between habitats (9.1% vs. 10.3%). However, plants in forest fragments faced a 4-fold increase in the damage by generalist leaf-cutting ants and a reduction of same magnitude in the damage by specialist hispines. Consistently with herbivory patterns, the density of leaf-cutting ant colonies was 6-fold greater and the abundance of hispines was 3-fold lower in forest fragments than in continuous forests. Although overall levels of damage varied greatly among plants, foliar damage had no effect on plant performance, suggesting high tolerance of *H. aurantiaca* to folivory. Surprisingly, daily microclimatic patterns were similar between habitats, as were density of *H. aurantiaca* shoots, leaf toughness and foliar condensed tannins. Disturbance-loving generalist herbivores may compensate the reduction in foliar damage caused by disturbance-sensitive specialist herbivores in tropical rainforest fragments, leaving levels of herbivory and their subsequent consequences on host performance similar between fragmented and continuous forests.

Key words: folivory; habitat fragmentation; *Heliconia aurantiaca*; herb; Lacandona rainforest; microclimate; plant-herbivore interactions; plant performance.

BECAUSE ECOLOGICAL INTERACTIONS ARE AN IMPORTANT FORCE structuring biological communities (Webb *et al*. 2002, Kembel & Hubbell 2006, Letcher 2010), understanding how human disturbance affect the ways organisms interact within and across trophic levels is a current priority in conservation research (Burslem *et al*. 2005). Most of the studies on ecological interactions conducted in fragmented tropical forests have focused on mutualistic interactions (Laurance 2005), with particular interest in pollination and seed dispersal (Ghazoul 2005). Antagonistic interactions such as insect herbivory and plant disease have been scantily examined (Laurance 2005), despite their well-known role on individual plant performance, plant population structure and the maintenance of local tree species diversity (see reviews by Coley & Barone 1996, Gilbert 2002, Marquis 2005, Burdon *et al*. 2006).

Plenty of evidence demonstrates that fragmented tropical forests are facing striking shifts in plant community structure, composition, and function (*e.g.,* Benítez-Malvido & Martínez-Ramos 2003, Laurance *et al*. 2006, 2007; Lopes *et al.* 2009, Santos *et al*. 2010, Lôbo et al. 2011). This floristic homogenization has been associated with physiological intolerance to altered microclimatic conditions, disruption of pollination and seed dispersal, as well as to selective logging, fire, hunting and other external processes that operate synergistically to increase the detrimental effects of forest fragmentation (*e.g.,* Tabarelli *et al*. 2004, Laurance & Useche 2009). More recently, shifts in herbivory has gained force in the debate on how altered ecological interactions can negatively affect plant communities and successional pathways in fragmented forests (*e.g.,* Urbas *et al*. 2007, Fáveri *et al*. 2008, Ruiz-Guerra *et al*. 2010). Particular attention has been paid to the negative consequences of the hyperabundance of disturbance-loving generalist herbivores in forest fragments (reviewed by Wirth *et al*. 2008), especially to leaf-cutting ants (*e.g.,* Rao 2000, Terborgh *et al*. 2001, Wirth *et al*. 2007, Meyer *et* *al*. 2009, Silva *et al*. 2009, Corrêa *et al*. 2010). These social insects cut leaves from hundreds of unrelated angiosperm species (Rico-Gray & Oliveira 2007), remove up to 13 percent of the standing leaf crop in a colony's territory per year (Wirth *et al*. 2003), and affect forest dynamics either by removing large amounts of leaf tissue from their host-plants or by creating canopy gaps on and around their nests (Corrêa *et al*. 2010, Meyer *et al*. 2011a). Although leaf-cutting ants may act as seed dispersers and partially compensate the absence of vertebrate frugivores in the South American savanna (Cerrado; Christianini & Oliveira 2009), their presence in neotropical fragmented forests has been closely associated with ecosystem decay of forest patches (*e.g.*, Terborgh *et al*. 2001, Wirth *et al*. 2008).

It is not yet clear, however, if leaf-cutting ants are representing an additional herbivory pressure in fragmented forests, or if they are compensating the foliar damage previously caused by many locally extirpated specialist herbivores (see Barbosa *et al*. 2005, Fonseca 2009). If they do represent an additional pressure, a highly palatable plant species should experience a significant increase in overall levels of damage in forest fragments compared to continuous ones. Potential negative consequences on host performance are predicted for plants in forest fragments as a result of leaf area reduction, but the magnitude of the consequences will depend on the ability of the host to tolerate herbivory (Strauss & Agrawal 1999). Alternatively, leaf-cutting ants might compensate the damage of declining specialist herbivores, resulting in no significant shifts in overall levels of herbivory in forest fragments. Hence, no changes in host performance are expected in forest fragments as a product of reduced leaf area. Testing these predictions was the main goal of our study.

We focused on the understory perennial tropical herb *Heliconia aurantiaca* (Heliconiaceae) and its most common insect herbivores: (1) hispine beetles, specialist on

Heliconiaceae and other Zingiberales; (2) caterpillars, variable in diet breadth; and (3) leaf-cutting ants, which are powerful generalist herbivores (see Methods). This study system allows not only an accurate estimation of the relative damage owing to each insect group, but also a reliable measure of host growth, survival, and reproductive success in natural conditions (see Methods). We monitored levels of foliar damage and host performance over two years in forest fragments and continuous forests and explored some physical and biological mechanisms that may jointly explain differences in herbivory patterns between habitats (*i.e.,* daily microclimatic patterns, host availability and quality). Particularly, we examined whether increased light incidence in the understory of forest fragments resulted in increased air and soil temperature and reduced air relative humidity. If so, we expected that habitat desiccation would decrease host density in forest fragments via reduction in seed germination and plant growth (Bruna 1999, Bruna et al. 2002), and increase leaf toughness and tannin content through greater light incidence (Coley & Barone 1996 and references therein). Finally, we predicted that the reduction in host availability and quality triggered by habitat desiccation would result in smaller levels of foliar attack in forest fragments, especially in damage by the specialist hispines.

METHODS

STUDY AREA.– This study was carried out in the Montes Azules Biosphere Reserve (REBIMA in Spanish), Southern Mexico, and the contiguous commonly-owned lands (‘*ejidos*’) of Chajul and Playón (16°06’ – 16°10’ N; 90°53’ – 90°58’ W). The REBIMA, created in 1978, is 330,000-ha in area and constitutes one of the main components of the Mesoamerican biodiversity hotspot (Myers *et al*. 2000, Figueroa *et al*. 2009). The primary vegetation type is lowland tropical rainforest, attaining 40 m in canopy height in alluvial terraces along main rivers (Siebe *et al*. 1995). Maximum and minimum annual temperatures average 30-34.5 °C (May-October) and 18-19.5 °C (November-April), respectively. Mean annual precipitation is 2,143 mm, but can reach up to 4,000 mm per year (García 1998); most of the annual rainfall is usually observed between June and September.

The REBIMA is bounded to its south by the Lacantún River, a 100-200 m wide watercourse that separate REBIMA's vast tracts of pristine old-growth forests from the severely fragmented landscape in which the Ejidos Chajul and Playón are embedded. Forest conversion to cattle pastures and croplands in the region started in mid 1970's. Today, a mosaic of small forest fragments, secondary vegetation, human settlements, croplands, pastures, and roads compose the landscape. Eight species of *Heliconia* have been recorded in the study area (Santos *et al*. 2009), but only three can be found in the shady conditions of the REBIMA's forest understory: *H. aurantiaca*, *H. librata*, and *H. vaginalis*. *H. aurantiaca* is also common in some forest fragments of the study area, so that we focused our study on this species.

STUDY SPECIES.– *Heliconia aurantiaca* is a perennial tropical understory herb native to Central America. Its rhizome is small compared to typical early-successional *Heliconia* species with high clonal reproduction via underground runners (*e.g., H. latispatha*, *H. collinsiana*, *H. metallica*), but it is similar to that of other understory *Heliconia* with very limited clonal reproduction (*e.g., H. acuminata*). Between February 2008 and June 2010 we observed the distribution, growth and reproduction of *H. aurantiaca* in our study area in Southern Mexico. The species occurs almost exclusively under the shaded conditions of forest understory; we rarely observed plants in canopy gaps, and when we did, they were along gap borders. Each plant usually presents less than ten shoots (mean five shoots per plants). Shoots sprout from the rhizome seasonally and usually last two years. Unless the plant face extremely high levels of damage (*e.g.,* coppicing or gopher attack), shoot sprouting take place after June (beginning of the rainy season), grow up during the subsequent six to eight months (reaching up to 2 m and 14 leaves), and then produce a single inflorescence (blooming takes place between February and April [dry season]). Shoots smaller than 1 m tall (or 8 leaves) have very low probability to produce the inflorescence. The inflorescence usually has four bracts and each bract produces up to six 1-d flowers. Flowers are gradually produced in around 2-d intervals and require hummingbird pollination for fertilization –we excluded 107 flowers from pollinators and none produced fruits. Inflorescences can last up to three months, so that shoots usually complete their single reproductive event at the end of the first year; the second, and less frequently, third year are marked by a gradual senescence process.

FOLIAR DAMAGE.– The foliage of the genus *Heliconia* is attacked by three major groups of insects: (1) hispines – most small Zingiberales-specialized chrysomelids, some specialized on *Heliconia* (Strong 1977a,b; Wilf *et al*. 2000); (2) caterpillars – represented by a broad gradient of body size and niche breadth, including those very large and specialized *Caligo* and *Opsiphanes* (owl butterflies) (De Vries 1987); and (3) leaf-cutting ants of the genus *Atta* – which is one of the most generalist herbivores in the Neotropics (Assis *et al*. 2002, Rico-Gray & Oliveira 2007). Each insect group produces characteristic feeding marks (Fig. S1), allowing an accurate estimation of their relative contribution to the overall level of damage (see Santos & Benítez-Malvido 2011). All three insect groups are known to feed on young and mature leaves of *Heliconia*, though adult hispines feed almost exclusively on young rolled-leaves (Strong 1977a,b).

To estimate the levels of foliar damage owing to insects on *H. aurantiaca*, we selected three sites in continuous forests and three sites in small (< 15 ha) forest fragments where the species occurred naturally (Table 1). In each site we arbitrarily chose six plants (more than 20 m apart to each other) and from each plant we randomly sampled 10 fully expanded leaves from all leaves of the plant (each plant usually had less than 50 leaves overall). Leaves were tagged to be monitored every three months from June 2008 to March 2010. During each trimester, the 360 tagged leaves were photographed using a 10-megapixel digital camera (Nikon Coolpix P80) and a blue background panel. Photographs were taken with macro lens (maximum focal length 84.2 mm) when leaves were flattened on the blue panel to avoid distortion. They were further processed using the image analysis software ASSESS (Lamari 2002) to quantify total leaf area and estimate the percentage of leaf area damaged by hispines, caterpillars, leaf-cutting ants, and unknown herbivores. A 2.5 cm x 2.5 cm scale was affixed to the blue panel to allow image calibration and the subsequent leaf area quantification. We averaged foliar attack per plant for the purposes of the analyses.

HERBIVORE ABUNDANCE.– To assess if forest fragmentation alters the local abundance of leaf-chewing insects associated with *Heliconia aurantiaca*, in September 2009 we randomly selected another set of 42 plants of *H. aurantiaca* in forest fragments and continuous forest (seven plants per site). We collected all hispines (larvae and adults) and caterpillars found on *Heliconia* shoots, including pseudostem, leaf blade, petiole, and inflorescence when present. Insects were placed in plastic pots containing alcohol (70%) and subsequently identified at the lowest possible taxonomic level. We also quantified the density of leaf-cutting ant nests in each site along 335-m long transects, following procedures described in Wirth *et al.* (2007). Transect length was determined on the basis of the maximum length of the smallest site (La Isla fragment, 335 m long). Because the sampling protocol included a fixed belt width of 10-m to each transect side, a total area of 0.67 ha (335 m x 20 m) was sampled in each site. We reported nest density per hectare to facilitate comparison with other studies.

HOST PERFORMANCE.– To assess the impact of total foliar damage on *H. aurantiaca* performance, we monitored host growth, survival, and reproduction success in each habitat type. Every three months we quantified the total number of shoots and flowers and recorded the survival status (alive or dead) of the 36 focal plants measured for foliar attack. Number of flowers was used instead of number of fruits or seeds because altered pollination patterns in forest fragments could confound the effect of foliar attack on seed and fruit output. Number of leaves of *H. aurantiaca* in our study area is strongly correlated with number of shoots ($R^2 = 0.92$; $N = 46$; $P < 0.0001$), then we reported host growth only in terms of number of shoots.

MICROCLIMATIC CONDITIONS.– To characterize the microclimate of forest fragments and continuous forests we installed a HOBO® data logger model U12 in each of the six study sites: three in forest fragments and three in continuous forest. Data loggers were positioned around a meter away from a randomly selected focal plant in each site, fixed at 1.3 m above the ground, and set to record simultaneous measures of air temperature, air relative humidity, light incidence and soil temperature (at 5 cm depth). Microclimatic data were recorded every hour during five consecutive days. We repeated this procedure during eight trimesters from September 2008 to June 2010 to evaluate whether the differences in the daily microclimatic patterns between habitats could vary across season. According to the HOBO manual, accuracy of measurements is ± 0.35 °C for temperature and ± 2.5 percent for relative humidity (up to 80% of relative humidity); accuracy is not provided by the manufacturer for light measurements in outdoor conditions, however.

HOST AVAILABILITY AND QUALITY.– We assessed host availability in April 2008, March 2009, and March 2010 by counting the number of conspecific shoots in a 10-m radius from focal plants in all six sites; the mean of the three years was used in the analyses. Host quality was evaluated in terms of foliar condensed tannins and leaf toughness. In January 2010 a segment of 10 cm x 10 cm of three undamaged, fully expanded leaves (fourth, fifth, and sixth leaves) was collected from 15 same-aged (2009 'cohort') no-reproducing shoots in each habitat type (one shoot per plant, five plants per site). Leaf segments were then processed in laboratory to quantify the absorbance of condensed tannins following Waterman and Mole (1994); absorbance was read in the spectrophotometer Thermo© Genesis 20 at 550 nm wavelength. Although absorbance does not provide a precise measure of tannin concentration, it gives a readily comparable index of the amount of tannins in our samples (Fáveri *et al*. 2008). To evaluate the effect of habitat type on leaf toughness we perforated the middle section of all fully expanded leaves presenting in the same shoots used for assessing condensed tannins. A 3-mm diameter rod was used to measure the force necessary to perforate the leaf blade (force was expressed in g/cm^2; see Boege 2005). Chemical and physical foliar characteristics were averaged per plant for the purposes of the analyses.

STATISTICAL ANALYSES.– We used generalized linear mixed model (GLMM) to test for differences in the levels of insect damage by distinct insect groups between habitats and among trimesters. Habitat type (between-subject factor), insect group (within-subject factor 1), trimester (within-subject factor 2) and all possible interactions were set as fixed effects, and focal plant (subject) was set as random effect (von Ende 2001). Levels of foliar damage (*i.e.,* the proportion of leaf area damaged) were arcsine-square-root transformed prior to analyses. We adopted GLMMs rather than other methods traditionally used to analyze repeated measures (*i.e.,* repeated-measure ANOVA, MANOVA, and profile analysis) because mixed models can handle many levels of the repeated measure factor and can be performed assuming different forms of the variance-covariance matrix (von Ende 2001). We used the restricted maximum likelihood method to separate the variance of fixed effects from that of the random effect, and Tukey-Kramer HSD (honestly significance difference) tests to compare means across treatment levels.

Differences in herbivore abundance between forest fragments and continuous forests were compared through one-way ANOVAs. Because abundance of hispines and caterpillars were too low to allow analysis at the plant level (many plants had none of these insects), we pooled abundance per site and ran ANOVAs with site as replicates ($N = 6$). Herbivore abundance was log transformed (log [x + 1]) before analyses. We used analyses of covariance (ANCOVAs) to test for the effect of foliar damage on the number of shoots and flowers in forest fragments and continuous forests. Number of shoots and flowers were log transformed and percentage of foliar damage was arcsine-square-root transformed before analyses.

We used GLMMs to test for differences in daily patterns of air temperature, relative humidity, light incidence, and soil temperature. Habitat type (between-subject factor), hour of the day (within-subject factor) and their interaction were set as fixed effect and site was set as random effect. Microclimatic analyses were run separately for each trimester. Relative humidity were arcsine-square-root transformed and light data was log transformed (log [x]) prior to analyses. Finally, we used one-way ANOVAs to compare shoot density (log-transformed), absorbance of condensed tannins, and leaf toughness between forest fragments and continuous forests. All analyses were performed in JMP 7 (SAS Institute Inc.). In all cases we report mean and standard error values for untransformed data.

RESULTS

FOLIAR DAMAGE.– Around 80 percent of the leaves showed some type of insect damage (72% in forest fragments and 88% in continuous forests). The most frequent damage was by hispines (63% of the leaves [52% in forest fragments and 78% in continuous forest]), followed by caterpillars (12% [10% vs. 14%]), leaf-cutting ants (8% [13% vs. 3%]), and unknown herbivores (8% [7% vs. 9%]). Overall, insects removed similar percentages of leaf area in forest fragments (9.1% ± 1.2%; mean ± SE) and continuous forests (10.3% ± 1.1%) (Table 2). However, the relative damage owing to each insect group clearly depended on habitat type (Table 2). While hispines reduced their average damage from 4.3 ± 0.4 percent in continuous forests to 1.1 ± 0.2 percent in forest fragments, damage by leaf-cutting ants increased from 1.5 ± 0.5 percent to 5.8 ± 0.9 percent (Fig. 1A). Damage by caterpillars tended to be lower in forest fragments than in continuous forests (2.8% ± 0.4% vs. 3.7% ± 0.9%), but this difference was not statistically significant (Fig. 1A). After 21 months the levels of insect damage increased by 5-fold (from 3.3% ± 0.6% to 15.8% ± 3.7%) irrespective of habitat type (Fig. 1B; Table 2), confirming that hispines, caterpillars, and leaf-cutting ants feed not only on young but also on mature leaves of *H. aurantiaca*.

HERBIVORE ABUNDANCE.– We collected a total of 28 caterpillars and hispines on the foliage of *H. aurantiaca* (8 in forest fragments and 20 in continuous forests). The abundance of hispines was significantly reduced by around 3-fold in forest fragments (from 4.6 ± 0.7 to 1.3 ± 0.3 individuals/site) ($F_{1,4} = 25.9$; $P < 0.01$; Fig. 2A), while the abundance of caterpillars did not differ between habitats (1.3 ± 0.6 vs. 2.0 ± 0.6 individuals/site) ($F_{1,4} = 0.61$; $P = 0.478$; Fig. 2B). Contrarily, the density of leaf-cutting ant colonies increased by 6-fold in forest fragments with respect to continuous forest (from 0.7 ± 0.3 to 4.0 ± 0.7 colonies/ha) ($F_{1,4} = 19.15$; $P < 0.05$; Fig. 2C).

EFFECT OF FOLIAR DAMAGE ON HOST PERFORMANCE.– On average, total foliar damage varied from 0.8 to 36.1 percent in forest fragments and from 2.9 to 28.8 percent in continuous forests. Plants presented an average size of 4.3 ± 0.9 shoots and reproductive plants produced 14.3 ± 2.0 flowers/year in forest fragments, compared to 3.8 ± 0.4 shoots and 17.2 ± 2.1 flowers/year in continuous forests. Neither number of shoots nor number of flowers correlated with foliar damage in forest fragments or continuous forests (Fig. S2; see Table S1 for ANCOVA results). Also, no plant died during the study period.

MICROCLIMATIC CONDITIONS.– Surprisingly, daily patterns of the four microclimatic variables analyzed were very similar between forest fragments and continuous forests (Table 3), regardless the trimester analyzed (see Table S2 for GLMMs results). There were few cases in which measures at a given time differed between habitats (Table S2), as indicated by the significant interaction habitat × time. However, the general pattern observed over the 21 months of monitoring was a surprising similar daily variation in microclimatic conditions of forest fragments and continuous forests (see Fig. 3 for a graphic representation of March 2009 data, which was a representative sample of the eight trimesters analyzed).

HOST AVAILABILITY AND QUALITY.– The local density of *H. aurantiaca* was more variable in forest fragments (2 – 39 shoots/314 m^2) than in continuous forests (2 – 28 shoots/314 m^2), but the average density did not differ between habitats (13.7 ± 2.2 vs. 9.8 ± 1.3 shoots/314 m^2) ($F_{1,34} = 0.01$; $P = 0.935$; Fig. S3A). Absorbance of condensed tannins was also similar between forest fragment and continuous forests (0.049 ± 0.001 vs. 0.052 ± 0.004) ($F_{1,28} = 0.38$; $P = 0.542$; Fig. S3B), as was leaf toughness (273 ± 4 g/cm^2 vs. 262 ± 6 g/cm^2) ($F_{1,28} = 2.35$; $P = 0.136$; Fig. S3C).

DISCUSSION

In the last decades many studies have documented shifts in ecological interactions in fragmented forests (Laurance 2005), but disruptions or alterations in antagonistic interactions such as herbivory and plant disease have been poorly examined despite their key role in community structure and ecosystem function (Benítez-Malvido & Lemus-Albor 2006, Wirth et al. 2008, Ruiz-Guerra *et al*. 2010). One of the main conclusions of our study is that generalist leaf-cutting ants may compensate the reduction in foliar damage caused by declining specialist hispines in tropical rainforest fragments, leaving levels of herbivory and their subsequent consequences on host performance similar between fragmented and continuous forests. This sort of functional compensation mediated by generalist herbivores highlights the importance of simultaneously examining herbivores with distinct diet breadth to understand patterns of herbivory in forest fragments (see Ewers & Didham 2006). If we had considered each insect group separately we would have found either increased, neutral or decreased herbivory in forest fragments. Differences in patterns of herbivory have been attributed to differences in ecosystem type, level of biological organization, host life form, and methods of measuring herbivory (Ruiz-Guerra *et al*. 2010). Here we demonstrated that all these factors being controlled, differences in herbivory may still arise from differences in herbivore diet.

Another important conclusion of this work is that the human-induced proliferation of generalist leaf-chewing herbivores appears to not be a major threat to *H. aurantiaca* in forest fragments considered, as plants grew and produced flowers regardless of habitat type and the high variation in foliar damage. Compared to late-successional herbivory-intolerant tree species, *H. aurantiaca* has lower leaf longevity, greater root:shoot ratio, and higher tillering ability, traits that are associated with increased tolerance to herbivory (Strauss & Agrawal 1999; see also Bruna *et al*. 2002, Bruna & Ribeiro 2005). Nevertheless, the potential high tolerance to foliar attack of *H. aurantiaca* does not mean that this understory herb will not face changes in performance as a consequence of altered antagonistic interactions in forest fragments. There are many herbivore species specialized in seeds or flowers, whose direct impacts on plant population structure are expected to be greater than those of leaf-chewing insects (Coley & Barone 1996). Also, our field observations indicate that burrowing gophers (Geomyidae) can kill the entire plant by consuming its rhizome (see also Baker *et al*. 2003), suggesting that changes in mammal herbivory might also be relevant for *H. aurantiaca* performance (gophers killed 11% [4 out 36] of our focal plants; all cases were recorded in continuous forests, but gophers also occur in forest fragments).

POTENTIAL MECHANISMS UNDERLYING HERBIVORE POPULATIONS.– Patterns of herbivory may result from differences in suitable microclimatic conditions for insect growth and reproduction, bottom-up and top-down controls of herbivore populations, and dispersal ability of herbivores (Wirth *et al*. 2008). According to our findings, the proliferation of generalist and the disappearance of specialist herbivores from forest fragments took place regardless the surprisingly suitable microclimatic conditions of these altered forests, suggesting that abiotic conditions play a secondary role in herbivore persistence in the forest fragments studied. At least for the *Heliconia*-insect system examined, the specialist hispines declined in forest fragments despite the similarity in host availability and quality, suggesting low importance of bottom-up control of hispine populations in forest fragments. The low dispersal ability of these insects could be another possibility to explain the low hispine number and damage in forest fragments (Strong 1977a,b; Fáveri *et al*. 2008), but the available evidence for the same study area indicate that these beetles take advantage of large clumps of early-successional *Heliconia* species to colonize the landscape matrix (Santos & Benítez-Malvido 2011). Therefore, the mechanisms underlying hispine disappearance from forest fragments appear to not be associated with microclimatic conditions, bottom-up control, and dispersal limitation.

We hypothesize that hispines are facing higher predation and/or parasitism pressure in forest fragments, either at larval or adult stages. Although this hypothesis of strengthen top-down control of herbivore populations in forest fragments is opposite to that of top-down relaxation induced by habitat fragmentation (*e.g.,* Kruess & Tscharntke 1994, Stouffer & Bierregaard 1995, Rao 2000, Terborgh *et al*. 2001, Sekercioglu *et al*. 2002, Almeida *et al*. 2008), it has been also examined and supported by several studies (*e.g.,* Vergara & Simonetti 2004, González-Gómez *et al*. 2006, Valladares *et al*. 2006, Simonetti *et al*. 2007, Lluch *et al*. 2009). Further studies are clearly needed to assess the role of predators and parasitoids in regulating populations of specialist herbivores in fragmented forests.

Unlike hispines, the processes underlying the proliferation of generalist leaf-cutting ants in forest fragments are well-known (Wirth *et al*. 2008). A clear mechanistic model has been proposed to explain the hyperabundance of leaf-cutting ants along forest edges in a severely fragmented landscape of the Brazilian Atlantic forest, where deforestation and fragmentation date back to 19th century. In that landscape, populations of leaf-cutting ants have faced a significant release from both bottom-up (increased abundance of pioneer trees, Urbas *et al*. 2007) and top-down controls (decreased phorid parasitism, Almeida *et al*. 2008), increasing in density by 5-11 times along forest edges (Wirth *et al*. 2007; Meyer *et al*. 2009). A similar process might be occurring in the small forest fragments of Southern Mexico, given that they had six times more ant colonies per hectare than the continuous forest. However, for *H. aurantiaca* in our study area, the hyperabundance of leaf-cutting ants does not represent an additional herbivory pressure. In fact, they ensure stability in the levels of foliar attack in forest fragments.

SOURCES OF VARIATION IN DAMAGE COMPENSATION.– The generalization of the functional compensation of generalist herbivores to other plant-herbivore systems should be drawn with caution. The first reason is that even generalist leaf-chewing herbivores have preference for certain host plant species (Bernays & Chapman 1994), so that the degree of compensation should be a function of their preference for the host plant considered. Our field observations indicate that *H. aurantiaca* is not a highly preferred component of *Atta* diet, as most of the attacked leaves recorded during the study period occurred because plants were too close to ant nests (< 20 m; B. A. Santos, personal observation). If these powerful herbivores were able to compensate the foliar damage of specialists in a low preferred host, it is likely that they impose increased folivory (*i.e.,* cause overcompensation) in more preferred plant species in forest fragments, potentially reducing their performance (Corrêa *et al*. 2010, Meyer *et al*. 2011b). Under-compensation (*i.e.,* lower folivory in forest fragments) is not expected in forest fragments dominated by these social herbivores (*e.g.,* Urbas et al. 2007) because their demand for leaf tissue is virtually greater than that of any other remaining specialist insect herbivore (Rico-Gray & Oliveira 2007). However, exceptions may occur during outbreaks of resistant specialists with high leaf tissue requirements, such as owl butterflies *Caligo* spp. in our study system.

Another confounding factor in the generalization of the functional compensation of generalist herbivores is that this type of herbivore can contract their diet in forest fragments (Falcão *et al*. 2011), increasing folivory pressure on particular groups of plants and potentially resulting in stronger overcompensation on them. Thirdly, the age and spatial configuration of the forest fragments studied may affect the establishment of any kind of plant-herbivore interactions (Ewers & Didham 2006), and therefore cause unexpected changes in the functional compensation mediated by generalist herbivores. We studied young (< 35-yr old), small (< 15 ha) forest fragments mostly surrounded by a mix of secondary vegetation, pasture and water. Different herbivory patterns may arise in forest patches with distinct characteristics (*e.g.,* older, more isolated; Ewers & Didham 2006).

Finally, resistance to foliar attack varies across plant species (Strauss *et al*. 2002), and even slightly overcompensation by generalists can have a negative effect on the performance of plants adapted to low folivory pressure in forest fragments (*e.g.,* late-successional slow-growing tree species; Coley & Barone 1996). In these herbivory-intolerant plants, the type of induced response to herbivory depends on molecular elicitors that are herbivore-specific (Kessler &

Baldwin 2002). The replacement of herbivores in forest fragments implies in replacement of elicitors, which may affect the metabolic re-configuration induced by herbivore wounding and the subsequent defensive strategy adopted by the plant (*i.e.,* to produce insect deterrent compounds [direct defense], volatile organic compounds to recruit herbivore predators [indirect defense], or to compensate for foliar damage [tolerance]) (Kessler & Baldwin 2002). Given that late-successional tree species are the main component structuring primary forests, further studies concerning these herbivore-intolerant plants are critical to produce a more comprehensive picture on how insect herbivory is altered in tropical fragmented forests.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

FIGURE S1. Feeding marks owing to hispines, caterpillars, and leaf-cutting ants on *H. aurantiaca*.

FIGURE S2. Relationship between foliar damage and host performance in forest fragments and continuous forest.

FIGURE S3. Host availability and quality in forest fragments and continuous forest.

TABLE S1. ANCOVA results applied to test for the effect of habitat type on the relationship between foliar damage and number of shoots and flowers.

TABLE S2. GLMM results fitted for microclimatic variables in forest fragments and continuous forest.

TABLE 1. *Characteristics of the three forest fragments and three tracts of continuous forest studied in Southern Mexico. REBIMA is the acronym (in Spanish) for the Montes Azules Biosphere Reserve. "Ejido" refers to commonly-owned lands.*

Site	Area	Coordinates	Altitude (m)	Location	Surronding matrix	Distance to old-growth continuous forest (m)	Estimated age in 2010 (yrs)
Forest fragments [a]							
Isla	3 ha	16°06'01" N 90°57'24" W	165	Ejido Chajul	Lacantun river, Chajul river, and cropland	> 200	35
Aforación	6 ha	16°08'40" N 90°54'11" W	158	Ejido Playón	Lacantun river and pasture	> 200	25
Piceno	< 15 ha	16°06'16" N 90°55'34" W	207	Ejido Chajul	Pasture and secondary forests	1700	25
Continuous forest [b]							
Tablero	-	16°07'33" N 90°56'04" W	172	REBIMA	Old-growth forest	-	-
Estación	-	16°06'54" N 90°56'50" W	177	REBIMA	Old-growth forest	-	-
Playón	-	16°09'32" N 90°54'20" W	164	REBIMA	Old-growth forest	-	-

[a] Pairwise distance of forest fragments varied from 3 to 8 km.

[b] Pairwise distance of continuous forests varied from 1.5 to 6 km.

TABLE 2. *Fixed effects of generalized linear mixed models fitted for repeated measures of foliar damage by insects on* Heliconia aurantiaca *in forest fragments and continuous forests of Southern Mexico.*

Model terms *	df	*F*-value	*P*-value	Model R^2
Herbivore damage				
Habitat	1, 34	0.203	0.6551	0.49
Trimester	7, 937	40.183	<0.0001	
Insect group	3, 930	72.527	<0.0001	
Habitat×Trimester	7, 937	0.201	0.9852	
Habitat×Insect group	3, 930	62.886	<0.0001	
Insect group×Trimester	21, 930	2.443	0.0003	
Habitat×Insect group×Trimester	21, 930	2.127	0.0023	

* Random effect “focal plant” accounted for 12.3% of the residual variance in herbivore damage.

TABLE 3. *Minimum and maximum values of air temperature, air relative humidity, light incidence, and soil temperature in forest fragments (FR) and continuous forest (CF) of Southern Mexico.*

Trimester	Air temperature (°C)		Air relative humidity (%)		Light incidence (lux)		Soil temperature (°C)	
	CF	FR	CF	FR	CF	FR	CF	FR
Sep-08	22.6 - 29.5	22.4 - 28.9	72.9 - 96.9	74.7 - 97.2	3.9 - 287.8	3.9 - 161.6	23.8 - 26.2	23.9 - 25.9
Dec-08	15.2 - 28.3	15.2 - 30.6	65.9 - 96.0	52.8 - 95.7	3.9 - 1202.3	3.9 - 674.1	19.1 - 23.1	19.3 - 23.5
Mar-09	16.3 - 31.8	16.5 - 31.7	47.0 - 94.4	39.5 - 95.0	3.9 - 555.8	3.9 - 752.9	20.1 - 24.1	19.6 - 24.2
Jun-09	21.6 - 34.3	21.8 - 34.2	57.5 - 95.0	42.1 - 93.7	3.9 - 1304.8	3.9 - 5656.6	24.5 - 31.7	24.2 - 30.6
Sep-09	22.3 - 29.0	22.2 - 29.6	78.8 - 96.1	70.6 - 95.2	3.9 - 926.3	3.9 - 926.3	23.1 - 27.4	23.3 - 26.2
Dec-09	16.0 - 26.1	16.1 - 28.7	82.3 - 96.0	72.2 - 95.6	3.9 - 256.2	3.9 - 208.9	19.4 - 27.4	19.3 - 25.9
Mar-10	15.2 - 35.7	15.5 - 36.8	36.1 - 95.5	35.6 - 95.2	3.9 - 2235.0	3.9 - 2074.0	18.9 - 25.3	19.8 - 24.7
Jun-10	22.8 - 34.5	22.4 - 34.4	69.4 - 94.6	62.8 - 94.7	3.9 - 390.2	3.9 - 1533.4	21.2 - 30.9	25.0 - 29.6
Mean	22.9	23.1	87.4	85.3	34.3	40.2	23.3	23.4

Figure legends

FIGURE 1. Foliar damage by insects (mean ± SE) on *Heliconia aurantiaca* in forest fragments (gray bars and circles) and continuous forests (white bars and circles) of Southern Mexico. (A) Relative damage by leaf-cutting ants (Ants), caterpillars (Cate), hispines (Hisp), and unknown insects (Unkn). (B) Cumulative damage since June 2008. Different letters in plot A indicate significant differences between habitats (Tukey-Kramer HSD test, $P < 0.05$).

FIGURE 2. Local abundance (means ± SE) of hispines (A), caterpillars (B), and leaf-cutting ant colonies (C) in forest fragments (gray bars) and continuous forests (white bars) of Southern Mexico. Different letters indicate significant differences between habitats (Tukey-Kramer HSD test, $P < 0.05$). Sites represent in a pooled sample of seven *Heliconia aurantiaca* plants.

FIGURE 3. Daily pattern of air temperature, air relative humidity, light incidence, and soil temperature in forest fragments (black dashed line) and continuous forest (solid gray line) of southern Mexico. Recording started on 12 March 2009 at 1300 h and ended on 17 March 2009 at 1300 h. Each curve was constructed by averaging measures from three sites per habitat type.

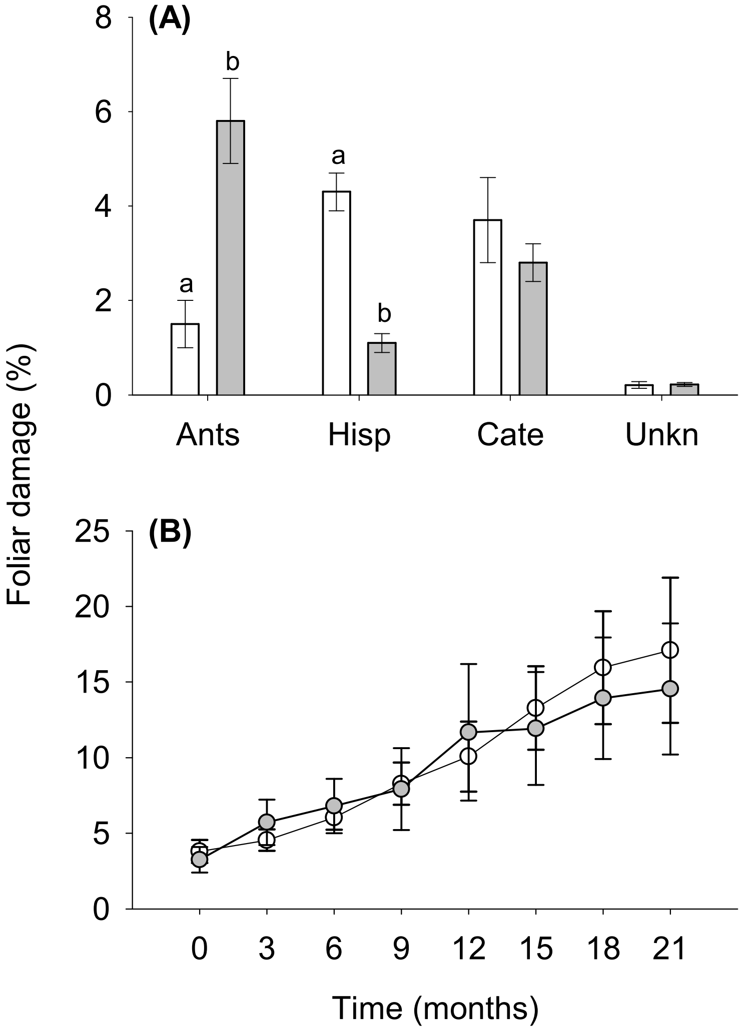
(A)
8
6
4
2
0
a
b
a
b
Ants
Hisp
Cate
Unkn
Foliar damage (%)
(B)
25
20
15
10
5
0
0
3
6
9
12
15
18
21
Time (months)

Figure 1.

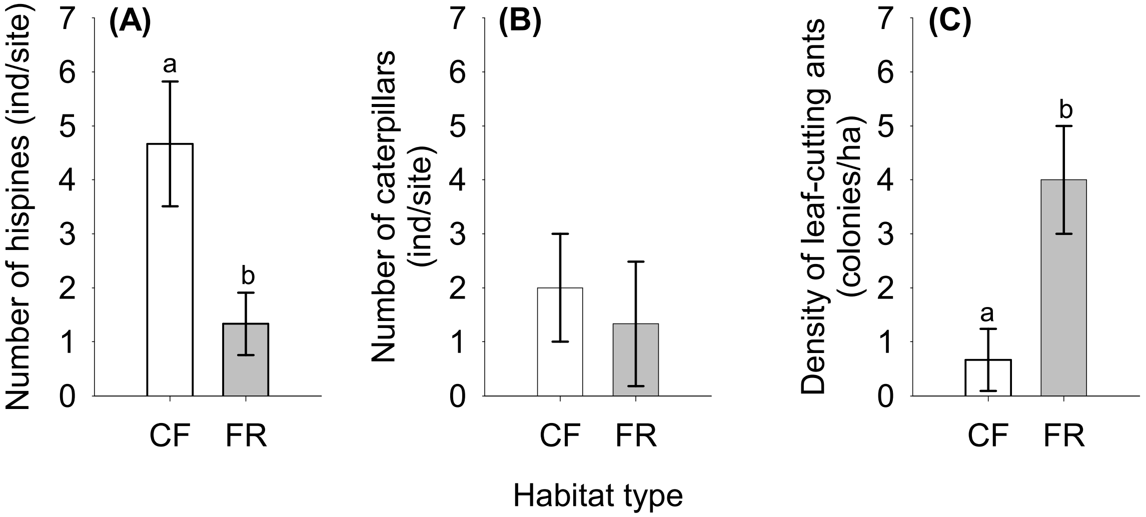
(A)
Number of hispines (ind/site)
0
1
2
3
4
5
6
7
a
b
CF
FR
(B)
Number of caterpillars (ind/site)
0
1
2
3
4
5
6
7
CF
FR
Habitat type
(C)
Density of leaf-cutting ants (colonies/ha)
0
1
2
3
4
5
6
7
a
b
CF
FR

Figure 2.

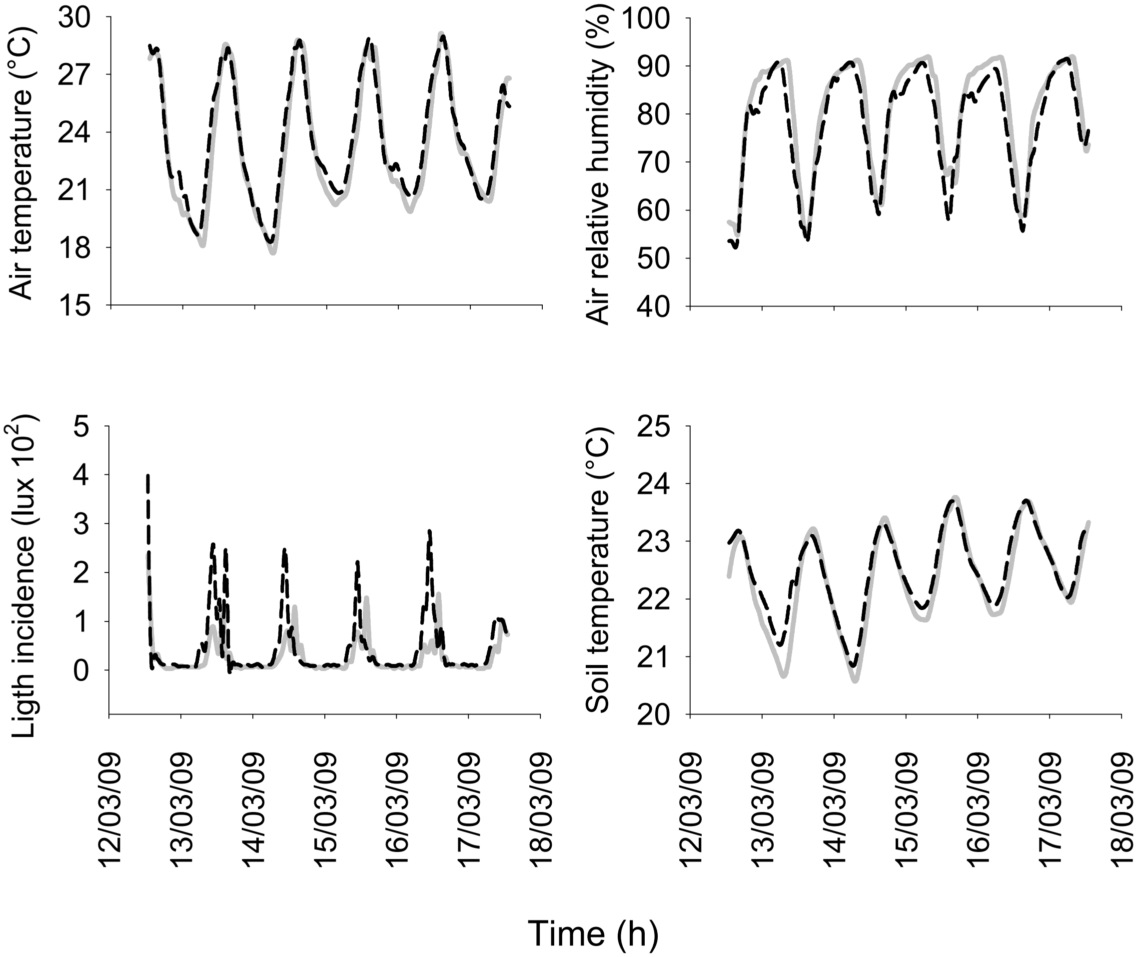
Air temperature (°C)
30
27
24
21
18
15
Air relative humidity (%)
100
90
80
70
60
50
40
Ligth incidence (lux 10²)
5
4
3
2
1
0
Soil temperature (°C)
25
24
23
22
21
20
12/03/09
13/03/09
14/03/09
15/03/09
16/03/09
17/03/09
18/03/09
Time (h)

Figure 3.

Figure S1. Feeding marks owing to hispine beetles (adult and larvae), caterpillars, and leaf-cutting ants on the foliage of *Heliconia aurantiaca* in Southern Mexico.

Hispine beetles: adults

* C. Staines, personal communication. *Cephaloleia* sp.1 belongs to the belti-complex, which contains 10 species scattered throughout Central America. The other two species belong to the instabilis-stenosoma complex, which has only two species extremely variable in coloration.

Hispine beetles: larvae

Caterpillars

Caligo uranus

Caligo memnon

Caterpillars


Tarchon felderi


Acharia cf. *stimulea*


Opsiphanes tamarindi tamarindi

Leaf-cutting ant: *Atta cephalotes*

Figure S2. Relationship between foliar damage and number of shoots (A) and flowers (B) of *Heliconia aurantiaca* in forest fragments (gray circles) and continuous forests (white circles) in Southern Mexico.

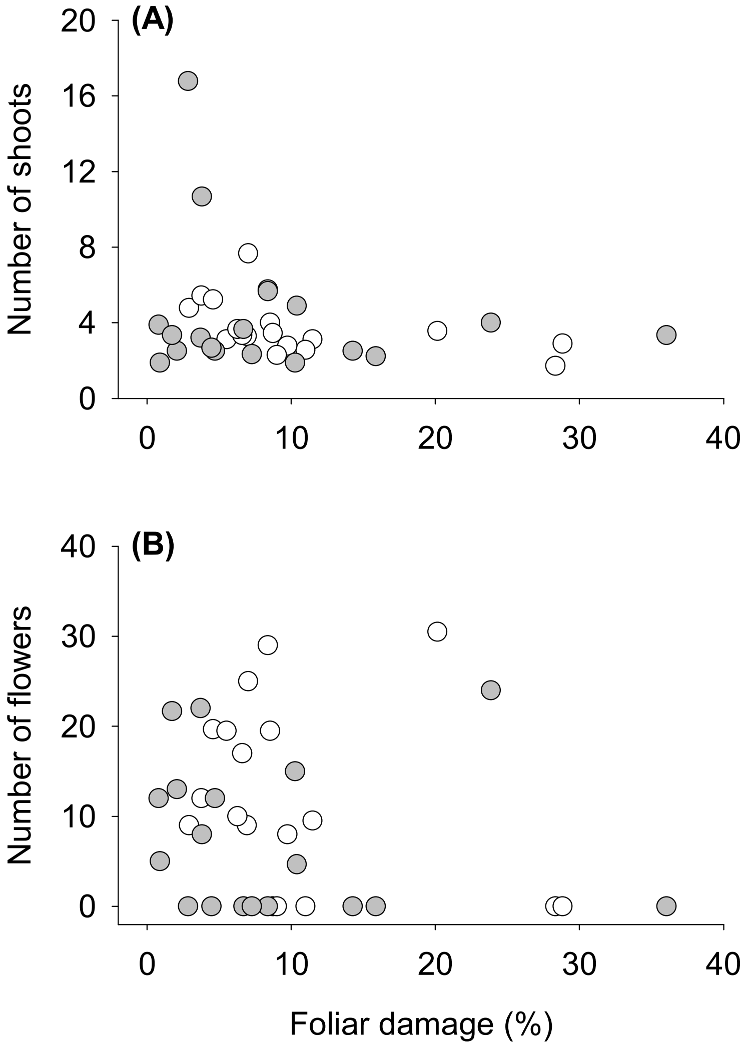

Figure S3. Host density (A), absorbance of foliar condensed tannins (B) and leaf toughness (C) (mean ± SE) of *Heliconia aurantiaca* in forest fragments (gray bars) and continuous forests (white bars) in Southern Mexico.

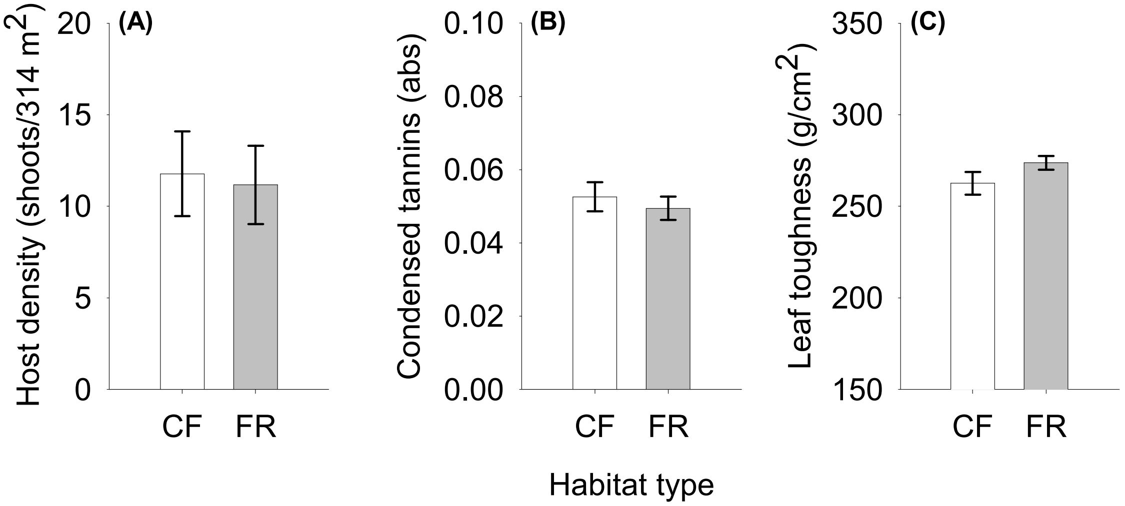

Table S1. Results of ANCOVA applied to test for the effect of habitat type on the relationship between foliar damage and number of shoots and flowers in *Heliconia aurantiaca*.

Model terms	df	*F*-ratio	*P*-value	Model R^2
Number of shoots				
Habitat	1, 32	0.165	0.687	0.06 (ns)
Foliar damage	1, 32	1.929	0.174	
Habitat X Foliar damage	1, 32	0.035	0.852	
Number of flowers				
Habitat	1, 32	2.376	0.133	0.11 (ns)
Foliar damage	1, 32	1.715	0.200	
Habitat X Foliar damage	1, 32	0.415	0.524	

Table S2. Fixed effects of generalized linear mixed models fitted for repeated measures of four microclimatic variables in forest fragments and continuous forest of Southern Mexico. The daily pattern of each variable was analyzed for eight trimesters separately; each spreadsheet shows results for a given trimester. Degrees of freedom were not always the same for each trimester because (1) one data logger was stolen, (2) another fell down after intense rainfall, and (3) some observations had to be excluded from the analyses due to local resident interference on data logger.

September 2008

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	1, 4	0.83	0.410	0.97
Time	69, 207	106.76	<0.0001	
Habitat X Time	69, 207	0.76	0.907	
Air relative humidity				
Habitat	1, 4	0.07	0.809	0.85
Time	69, 207	15.07	<0.0001	
Habitat X Time	69, 207	0.43	0.430	
Light incidence				
Habitat	1, 4	0.05	0.841	0.78
Time	69, 207	6.95	<0.0001	
Habitat X Time	69, 207	0.54	0.545	
Soil temperature				
Habitat	1, 4	0.39	0.387	0.94
Time	69, 207	48.32	<0.0001	
Habitat X Time	69, 207	0.71	0.953	

December 2008

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	1, 4	0.90	0.396	0.97
Time	120, 456	139.70	<0.0001	
Habitat X Time	120, 456	1.24	0.062	
Air relative humidity				
Habitat	1, 4	3.07	0.154	0.95
Time	120, 456	68.30	<0.0001	
Habitat X Time	120, 456	2.65	<0.0001	
Light incidence				
Habitat	1, 4	0.23	0.659	0.72
Time	120, 456	5.00	<0.0001	
Habitat X Time	120, 456	1.16	0.143	
Soil temperature				
Habitat	1, 4	0.35	0.586	0.57
Time	120, 456	1.64	<0.001	
Habitat X Time	120, 456	0.93	0.671	

March 2009

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	1, 4	0.48	0.526	0.95
Time	120, 458	76.13	<0.0001	
Habitat X Time	120, 458	1.12	0.200	
Air relative humidity				
Habitat	1, 4	0.94	0.386	0.93
Time	120, 458	47.75	<0.0001	
Habitat X Time	120, 458	1.03	0.403	
Light incidence				
Habitat	1, 4	1.36	0.308	0.82
Time	120, 458	14.41	<0.0001	
Habitat X Time	120, 458	1.18	0.123	
Soil temperature				
Habitat	1, 4	0.09	0.775	0.95
Time	120, 458	73.95	<0.0001	
Habitat X Time	120, 458	1.16	0.144	

June 2009

Note: A data logger was stolen from a forest fragment (Aforación)

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	1, 3	1.66	0.288	0.93
Time	120, 360	43.40	<0.0001	
Habitat X Time	120, 360	1.07	0.319	
Air relative humidity				
Habitat	1, 3	1.02	0.387	0.94
Time	120, 360	41.17	<0.0001	
Habitat X Time	120, 360	0.81	0.909	
Light incidence				
Habitat	1, 3	0.01	0.967	0.80
Time	120, 360	10.45	<0.0001	
Habitat X Time	120, 360	1.40	<0.01	
Soil temperature				
Habitat	1, 3	0.04	0.859	0.92
Time	120, 360	28.27	<0.0001	
Habitat X Time	120, 360	2.00	<0.0001	

September 2009

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	1, 4	0.67	0.46	0.97
Time	120, 418	125.74	<0.0001	
Habitat X Time	120, 418	1.16	0.143	
Air relative humidity				
Habitat	1, 4	1.92	0.238	0.83
Time	120, 418	11.77	<0.0001	
Habitat X Time	120, 418	1.13	0.191	
Light incidence				
Habitat	1, 4	0.22	0.661	0.70
Time	120, 418	4.47	<0.0001	
Habitat X Time	120, 418	0.26	0.923	
Soil temperature				
Habitat	1, 4	0.87	0.403	0.88
Time	120, 418	1.72	<0.0001	
Habitat X Time	120, 418	0.89	0.763	

December 2009

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	1, 4	7.26	0.054	0.98
Time	120, 455	268.39	<0.0001	
Habitat X Time	120, 455	1.01	0.452	
Air relative humidity				
Habitat	1, 4	3.78	0.123	0.89
Time	120, 455	27.81	<0.0001	
Habitat X Time	120, 455	1.85	<0.0001	
Light incidence				
Habitat	1, 4	0.19	0.684	0.75
Time	120, 455	3.48	<0.0001	
Habitat X Time	120, 455	152.00	<0.01	
Soil temperature				
Habitat	1, 4	0.12	0.751	0.98
Time	120, 455	227.45	<0.0001	
Habitat X Time	120, 455	0.40	0.965	

March 2010

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	1, 4	1.75	0.256	0.96
Time	120, 416	239.04	<0.0001	
Habitat X Time	120, 416	0.67	0.995	
Air relative humidity				
Habitat	1, 4	1.95	0.235	0.95
Time	120, 416	60.86	<0.0001	
Habitat X Time	120, 416	1.39	<0.01	
Light incidence				
Habitat	1, 4	1.02	0.370	0.85
Time	120, 416	6.16	<0.0001	
Habitat X Time	120, 416	1.12	0.213	
Soil temperature				
Habitat	1, 4	1.95	0.234	0.89
Time	120, 416	27.88	<0.0001	
Habitat X Time	120, 416	0.41	0.997	

June 2010

Model terms	df	*F*-ratio	*P*-value	Model R^2
Air temperature				
Habitat	1, 4	0.05	0.834	0.98
Time	95, 315	207.91	<0.0001	
Habitat X Time	95, 315	0.78	0.928	
Air relative humidity				
Habitat	1, 4	3.46	0.136	0.96
Time	95, 315	70.45	<0.0001	
Habitat X Time	95, 315	1.12	0.229	
Light incidence				
Habitat	1, 4	10.87	<0.05	0.73
Time	95, 315	7.45	<0.0001	
Habitat X Time	95, 315	0.96	0.571	
Soil temperature				
Habitat	1, 4	0.97	0.379	0.96
Time	95, 315	6.18	<0.0001	
Habitat X Time	95, 315	0.96	0.593	

CAPITULO V

RH: Fungal infection in fragmented forests

Increased leaf fungal infection in fragmented forests

(Enviado a Conservation Biology)

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Keywords: habitat fragmentation, *Heliconia*, herbs, Lacandona, leaf disease, Mexico, plant-pathogen interaction.

Abstract

Antagonistic biotic interactions such as plant-pathogen associations have been scantly studied in fragmented forests despite their direct implications for biodiversity and ecosystem functioning. Here we monitored fungal infection on the foliage of the native understory perennial herb *Heliconia aurantiaca* in the region of Chajul, Southern Mexico, to test the hypothesis that human disturbance favors disease proliferation in tropical rainforest fragments. At the beginning of the study, plants presented similar levels of foliar damage in forest fragments and nearby continuous forests, but after one year fungal infection increased more in forest fragments, resulting at the end of the study in an average increase of 80% in the cumulative damage in forest fragments. Nevertheless, plants grew up, survived, and reproduced irrespective of the level of pathogen damage, supporting previous evidence emphasizing the high tolerance of *H. aurantiaca* to foliar damage. As most of the leaf fungal pathogens attacking *Heliconia* are generalists, the increased pathogen pressure in forest fragments is likely to hold for other co-occurring plant species, with potential negative consequences for the performance of species with low tolerance to biotic damage (e.g. most of old-growth forest tree species). Because pathogen damage has been proved to increase along road edges and degraded riparian vegetation in the same study area, the proliferation of plant infectious diseases seems to be a widespread phenomenon in the region of Chajul. This process might be in progress in other tropical areas in which forest has been converted to pastures and croplands.

Introduction

Disruptions in biotic interactions are considered a major cause of biodiversity loss in fragmented tropical forests (Laurance 2005). Although antagonistic interactions such as that observed between plants and pathogens have contributed for the diversification of life on Earth (Gilbert 2002; Burdon & Thrall 2009) and directly influence agriculture and its associated economic profits (Pimentel et al. 2001; Agrios 2005), our understanding about how plant-pathogen interactions are altered in fragmented forests is still very elementary (Benítez-Malvido & Lemus-Albor 2006). Fungi are the major causal agents of plant infectious diseases and jointly with insects comprise one of the major threats to wild and cultivated plant species worldwide (Coley & Barone 1996; Desprez-Loustau et al. 2007). Assessing the magnitude of fungal attack on plants persisting in fragmented landscapes is therefore critical for improving the success of conservation initiatives (Anderson et al. 2004).

There are several reasons to expect that human disturbance favors the proliferation of plant diseases in fragmented tropical rainforests (Benítez-Malvido & Lemus-Albor 2006). Main reasons include environmental stress triggered by forest destruction that may debilitate the host plants and increase their susceptibility to infection; proliferation of fast-growing poorly defended plant species that may scale up disease prevalence to the community level; and introduction of invasive and novel pathogens due to road construction, agriculture, and forestry. In addition, a recent review by Keesing et al. (2010) suggests that biodiversity loss owing to land-use changes, agricultural intensification, food industry changes and other anthropogenic causes increase disease emergence and transmission. Here we used the native understory herb *H. aurantiaca* to test the hypothesis that human disturbance favors disease proliferation in tropical rainforest fragments. Also, we evaluated the relationships between pathogen attack and plant growth, survival, and reproductive success, to assess the consequences of fungal damage on plant performance. We carried out our surveys in the region of Chajul, Southern Mexico, where deforestation and forest conversion to pasture and croplands is intense, as observed in other neotropical regions.

Methods

Data collection

The herbaceous species *H. aurantiaca* belongs to the banana-related family Heliconiaceae, is native to Central America and commonly found in the shaded understory of fragmented and continuous forests of Southern Mexico (Santos et al. 2009; it is rare in canopy gaps; see appendix S1 for notes on the natural history of the species). To estimate the levels of pathogen damage on the foliage of *H. aurantiaca*, we selected three continuous forests and three small (< 15 ha) forest fragments where the species naturally occurred (see Table S1 for detailed information on fragment size, age, matrix, distance to nearest continuous forest and other geographic data). In each site we randomly chose six plants and from each plant we randomly sampled 10 fully expanded leaves (360 in total). Leaves were tagged and monitored every three months from June 2008 to March 2010. During each trimester, we photographed the surviving leaves with a 10-megapixel digital camera (Nikon Coolpix P80; macro lens with maximum focal length of 84.2 mm) and a blue background panel. Then, we processed the photos with the image analysis software ASSESS (Lamari 2002) to quantify total leaf area and estimate the percentage of leaf area damaged by pathogens.

Before taking the photos, we affixed a 2.5 cm x 2.5 cm scale to the blue panel to allow image calibration and leaf area quantification. We averaged foliar damage per plant for the purposes of the analyses.

To assess the impact of overall pathogen damage on *H. aurantiaca* performance, we monitored host growth, survival, and reproductive success in forest fragments and continuous forests during the same period. Every three months we quantified the total number of shoots and flowers and recorded the survival status (alive or dead) of the 36 focal plants measured for foliar attack. We used number of flowers instead of number of fruits or seeds because altered pollination patterns in forest fragments could cofound the effect of foliar attack on seed and fruit output. Number of leaves of *H. aurantiaca* in our study area is strongly correlated with number of shoots ($R^2 = 0.92$; $N = 46$; $P < 0.0001$), then we reported host growth only in terms of number of shoots.

Statistical analyses

We used generalized linear mixed models (GLMM) to test for differences in rates of fungal infection and cumulative damage between forest fragments and continuous forests. Habitat type (between-subject factor), time (within-subject factor) and their interaction were set as fixed effects, and focal plant (subject) was set as random effect (Von Ende 2001). The response variable (proportion of leaf area damaged) was arcsine-square-root transformed prior to analyses. We used the restricted maximum likelihood method to separate the variance of fixed effects from that of the random effect.

We used one-way analyses of variance (ANOVAs) to compare the number of shoots and flowers between habitats, and analyses of covariance (ANCOVAs) to test for the effect of habitat type on the relationship between pathogen damage and the number of shoots and flowers. In all ANOVAs and ANCOVAs we used the mean value of the three variables, averaged from the eight trimesters considered. Number of shoots and flowers were log transformed (log [x+1]) and percentage of foliar damage was arcsine-square-root transformed before analyses. We performed all analyses in JMP 7 (SAS Institute) and reported mean and standard error values for untransformed data.

Results

About 36% percent of the *H. aurantiaca* leaves were damaged by pathogens (34% in forest fragments and 38% in continuous forest). The percentage of leaf area infected started with near-zero values and increased at low rates (< 1% per month) during the first 12 months, regardless habitat type. However, after this period, fungal infection increased exponentially more in forest fragments than in continuous forests, resulting at the end of the study in an increase of about 80% in the overall levels of pathogen damage in forest fragments compared to continuous forest (Table 1; Fig. 1).

During the 21 months of monitoring, the mean level of pathogen damage per plant varied from 0.3% to 33.2% in forest fragments and from 0.03% to 18.7% in continuous forests. Plants presented an average size of 4.3 (SE 0.9) shoots in forest fragments and 3.8 (0.4) shoots in continuous forest ($F_{1,34} = 0.003$; $P = 0.955$). Flower production per year was 13.7 (2.4) in forest fragments ($n = 10$ reproductive plants) and 16.7 (2.1) in continuous forests ($n = 13$), but this difference was not statistically significant ($F_{1,34} = 1.65$; $P = 0.207$). Also, none of these plant performance measures correlated with pathogen damage in forest fragments or continuous forest (see Table S2 for ANCOVA results), and no plant died during the study period.

Discussion

Although an increasingly number of studies highlights the potential proliferation of animal and plant diseases − emerging or not − as a product of human disturbance (reviewed by Anderson et al. 2004; Keesling et al. 2010), there is very little information on disease incidence and severity in fragmented tropical rainforests (Benítez-Malvido et al. 1999, 2005; Benítez-Malvido & Lemus-Albor 2005). Our findings with the native understory perennial herb *Heliconia aurantiaca* support the hypothesis of increased pathogen pressure in human-disturbed habitats. Particularly, our results indicate that fungal infection can be greater in tropical rainforest fragments than in nearby continuous forest. This phenomenon had not yet been empirically demonstrated − previous studies measured only standing levels of pathogen damage − and is expected to have negative effects upon biodiversity and ecosystem function (Anderson et al. 2004; Benítez-Malvido & Lemus-Albor 2006).

Nevertheless, at least for *H. aurantiaca*, our observations suggest that the human-induced increase in pathogen pressure was not enough to reduce its performance in forest fragments. This can be explained by the high number of *H. aurantiaca* traits associated with high tolerance to biotic damage. Compared with late-successional tropical tree species, *H. aurantiaca* has lower leaf longevity, greater root:shoot ratio, and higher tillering ability (see also Bruna et al. 2002 and Bruna & Ribeiro 2005), which confer greater ability to compensate the biotic damage (Strauss & Agrawal 1999). On the other hand, late-successional tree species typical of undisturbed forests usually have greater ability to avoid or reduce biotic damage, but lower ability to compensate it (Coley & Barone 1996). For this group of species, an increase of 80% in the level of pathogen damage such as that we observed on *H. aurantiaca* is likely to incur in significant reductions in plant performance

Although the generality of the pattern observed in *H. aurantiaca* to the entire remaining biota is currently not viable due to the limited number of studies, at least in the forest fragments studied the increasing pathogen pressure is expected to scale up to the community level. Most of the *Heliconia* pathogens are generalist fungal pathogens that also attack many unrelated angiosperm species, including dicotyledonous (Assis et al. 2002; Santos 2011). In addition, the angiosperms that usually thrive in forest fragments are fast-growing pioneer species that are poorly defended against herbivores and pathogens and that face greater levels of biotic damage than do slow-growing late-successional species (Coley & Barone 1996; Laurance et al. 2006; Ruiz-Guerra et al. 2010; Tabarelli et al. 2010). Nevertheless, more studies evaluating the spatiotemporal variation in fungal damage on locally abundant species would help to confirm whether disease prevalence in forest fragments is a community-wide phenomenon.

The physical and biological processes underlying the differences in pathogen pressure between forest fragments and continuous forest also deserve more attention. Habitat desiccation triggered by deforestation and forest fragmentation can increase plant susceptibility to fungal infection and might explain the greater fungal damage on *H. aurantiaca* in forest fragments (see Agrios 2005). However, previous evidence showed that the understory of the studied forest fragments and continuous forests presented similar daily microclimatic patterns of light incidence, air and soil temperature, and air relative humidity (Santos 2011). Another possibility might be that plants were less defended and occurred at greater densities in forest fragments than continuous forest, but levels of leaf toughness, foliar condensed tannins and density of conspecific shoots in a 10-m radius were also similar between habitats (Santos 2011). We hypothesize that increased fungal damage on *H. aurantiaca* in forest fragments is likely to be driven by a combination of greater inbreeding depression of host plants in forest fragments (fragmentation can increase inbreeding and inbred plants usually are more susceptible to infection; Young et al. 1996; Bello-Bedoy & Núñez-Farfán 2011); introduction of invasive, more virulent pathogens from the abutting crop fields and pastures (Anderson et al. 2004; Benítez-Malvido & Lemus-Albor 2006); and/or greater availability of alternative hosts, particularly fast-growing pioneer species (Laurance et al. 2006; Tabarelli et al. 2010).

Although the mechanisms underlying the proliferation of leaf diseases in forest fragments are still uncertain, the pattern is clear enough to put plant-pathogen interactions in a more visible position in conservation projects (see also Anderson et al. 2004, Nichols & Gómez 2011). In our study area the prevalence of plant infectious diseases takes place not only in the forest fragments, but also along road edges and degraded riparian corridors scattered throughout the landscape matrix (Santos & Benítez-Malvido 2011). This indicates that the proliferation of plant infectious diseases may be a widespread phenomenon in our study area. Given that the model of deforestation and forest conversion in Southern Mexico is representative of other tropical areas, it is likely that this phenomenon is underway in other tropical forests.

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Supporting information

Natural history of *H. aurantiaca* (Appendix 1), characteristics of the study sites (Table S1) and the results of the ANCOVAs (Table S2) are available online.

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Table 1. Fixed effects of generalized linear mixed models fitted for pathogen damage on *Heliconia aurantiaca* in the region of Chajul, Southern Mexico.

Model terms	df	*F*-ratio	*P*-value	Model R^2 (%)
Rates of fungal infection				
habitat	1, 34	3.281	0.078	45.4
time	6, 182	23.874	< 0.0001	
habitat × time	6, 182	0.517	0.794	
Cumulative fungal damage				
habitat	1, 34	4.445	0.042	73.6
time	7, 210	49.092	< 0.0001	
habitat × time	7, 210	3.157	0.003	

Figure legend

Figure 1. Cumulative fungal damage on the foliage of *Heliconia aurantiaca* in forest fragments (black circles) and continuous forests (white circles) at the region of Chajul, Southern Mexico. Time "0" represents June 2008; bars indicate standard error of the mean. Fit of forest fragment data, y = exp (0.163*x); fit of continuous forest data, y = exp (0.1308*x).

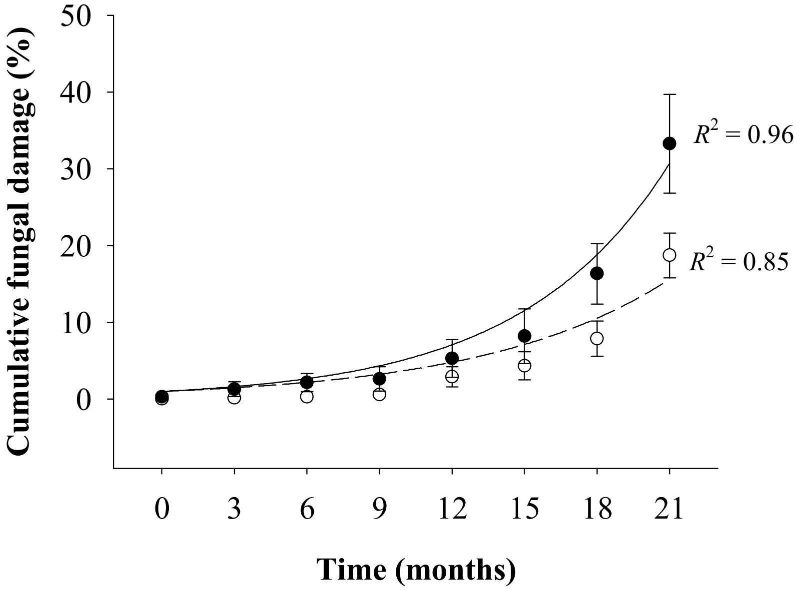
Cumulative fungal damage (%)
50
40
30
20
10
0
$R^2 = 0.96$
$R^2 = 0.85$
0
3
6
9
12
15
18
21
Time (months)

Figure 1.

Appendix S1. Notes on the natural history of *Heliconia aurantiaca* in southern Mexico, with emphasis on its growth and reproduction.

Heliconia aurantiaca is a perennial tropical understory herb native to Central America. Its rhizome is small compared to typical early-successional *Heliconia* species with high clonal reproduction via underground runners (*e.g., H. latispatha*, *H. collinsiana*, *H. metallica*), but it is similar to that of other understory *Heliconia* with very limited clonal reproduction (*e.g., H. acuminata*). Between February 2008 and June 2010 we observed the distribution, growth and reproduction of *H. aurantiaca* in our study area in Southern Mexico. The species occurs almost exclusively under the shaded conditions of forest understory; we rarely observed plants in canopy gaps, and when we did, they were along gap borders. Each plant usually presents less than ten shoots (mean five shoots per plants). Shoots sprout from the rhizome seasonally and usually last two years. Unless the plant face extremely high levels of damage (*e.g.,* coppicing or gopher attack), shoot sprouting take place after June (beginning of the rainy season), grow up during the subsequent six to eight months (reaching up to 2 m and 14 leaves), and then produce a single inflorescence (blooming takes place between February and April [dry season]). Shoots smaller than 1 m tall (or 8 leaves) have very low probability to produce the inflorescence. The inflorescence usually has four bracts and each bract produces up to six 1-d flowers. Flowers are gradually produced in around 2-d intervals and require hummingbird pollination for fertilization –we excluded 107 flowers from pollinators and none produced fruits. Inflorescences can last up to three months, so that shoots usually complete their single reproductive event at the end of the first year; the second, and less frequently, third year are marked by a gradual senescence process.

Table S1. Characteristics of the three forest fragments and three tracts of continuous forest studied in Southern Mexico. REBIMA is the acronym (in Spanish) for the Montes Azules Biosphere Reserve. “Ejido” refers to commonly-owned lands.

Site	Area	Coordinates	Altitude (m)	Location	Surronding matrix	Distance to old-growth continuous forest (m)	Estimated age in 2010 (yrs)
Forest fragments [a]							
Isla	3 ha	16°06'01" N 90°57'24" W	165	Ejido Chajul	Lacantun river, Chajul river, and cropland	> 200	35
Aforación	6 ha	16°08'40" N 90°54'11" W	158	Ejido Playón	Lacantun river and pasture	> 200	25
Piceno	< 15 ha	16°06'16" N 90°55'34" W	207	Ejido Chajul	Pasture and secondary forests	1700	25
Continuous forest [b]							
Tablero	-	16°07'33" N 90°56'04" W	172	REBIMA	Old-growth forest	-	-
Estación	-	16°06'54" N 90°56'50" W	177	REBIMA	Old-growth forest	-	-
Playón	-	16°09'32" N 90°54'20" W	164	REBIMA	Old-growth forest	-	-

[a] Pairwise distance of forest fragments varied from 3 to 8 km.

[b] Pairwise distance of continuous forests varied from 1.5 to 6 km.

Table S2. Result of analyses of covariance applied to test the effect of habitat type on the relationship between fungal damage and number of shoots and flowers of *Heliconia aurantiaca*.

Model terms	df	*F*-ratio	*P*-value	Model R^2 (%)
Number of shoots				
Habitat	1, 32	0.008	0.928	10.0 (ns)
Fungal damage	1, 32	0.009	0.925	
Habitat × Fungal damage	1, 32	1.394	0.246	
Number of flowers				
Habitat	1, 32	2.066	0.160	6.2 (ns)
Fungal damage	1, 32	0.510	0.480	
Habitat × Fungal damage	1, 32	0.489	0.489	

DISCUSIÓN GENERAL

Entender cómo las plantas interactúan con sus enemigos naturales ha sido un tema central en estudios de ecología y evolución (Ehrlich & Raven 1964, Coley & Barone 1996, Strauss & Agrawal 1999, Gilbert 2002, Strauss et al. 2002, Marquis 2005, Núñez-Farfán et al. 2007, Burdon & Thrall 2009). En selvas tropicales, las plantas constituyen la base de una de las redes tróficas más complejas del planeta y son atacadas principalmente por insectos y hongos (Coley & Barone 1996, García-Guzmán & Morales 2007). Aunque la herbivoría y las enfermedades foliares afectan el desempeño de las plantas hospederas, la estructura poblacional de éstas, la organización de las comunidades biológicas, los procesos ecosistémicos y la evolución de nuevas especies (ver revisiones de Burdon et al. 1989, Coley & Barone 1996, Gilbert 2002, Marquis 2005), se sabe muy poco acerca de cómo esas interacciones pueden ser alteradas en selvas secundarias y degradadas (Laurance 2005, Wirth et al. 2008, Ruiz-Guerra et al. 2010).

Los principales resultados de esta tesis sugieren que la perturbación humana de selvas altas perennifolias beneficia a los herbívoros generalistas en detrimento de los especialistas y favorece la proliferación de enfermedades foliares, lo que corrobora dos hipótesis surgidas recientemente acerca de posibles cambios en las interacciones planta-herbívoro y planta-patógeno en selvas fragmentadas (Benítez-Malvido & Lemus-Albor 2006, Wirth et al. 2008). Asimismo, este estudio demuestra que la proliferación de herbívoros generalistas no siempre resulta en un aumento en el nivel total de daño foliar, ni en la subsecuente reducción en el desempeño de la planta hospedera. Este mecanismo de compensación funcional mediado por los herbívoros generalistas aún no había sido descrito en la literatura, pues ningún estudio había considerado, en el mismo sistema, el daño relativo causado por herbívoros con diferentes amplitudes de dieta. Los resultados de esta tesis también sugieren que aunque las condiciones físicas, la calidad y la disponibilidad de hospederos puedan afectar los niveles de herbivoría, el factor ecológico más importante en este proceso es la abundancia de herbívoros, lo que ayuda a entender las causas de alteraciones en las relaciones planta-herbívoro provocadas por el hombre, poco exploradas hasta el momento. Finalmente, los resultados indican un alto potencial para el aprovechamiento de heliconias nativas en las selvas secundarias y degradadas de la región de Chajul, Chiapas.

Microclima y daño biótico

Es bien sabido que los efectos deletéreos de la fragmentación en selvas altas perennifolias empiezan por el súbito cambio microclimático cerca del borde (Murcia 1995), el cual lleva a la proliferación de plantas pioneras y al empobrecimiento taxonómico y funcional de la comunidad de plantas remanente (Laurance et al. 2006, 2007; Girão et al. 2007, Santos et al. 2008, 2010; Lopes et al. 2009, Tabarelli et al. 2010). Los herbívoros, patógenos, polinizadores, dispersores y depredadores de semillas que dependen directamente de las plantas vulnerables también son afectados negativamente (Laurance 2005). Muchos estudios discuten el papel de las condiciones microclimáticas en la dinámica de fragmentos forestales, pero hasta la fecha menos de 20 trabajos han medido explícitamente las condiciones microclimáticas en fragmentos de selva (e.g. Kapos 1989, Williams-Linera 1990, Camargo & Kapos 1995, Williams-Linera et al. 1998, Didham & Lawton 1999, Newmark *et al*. 2001, Pohlman *et al*. 2007, Pinto et al. 2010, González-Di Pierro et al. 2011). Hay una tendencia de desecamiento del hábitat tras la perturbación humana, pero todavía no se puede hacer ninguna generalización en el espacio y el tiempo porque los estudios están sesgados hacia pocos fragmentos casi siempre con menos de 10 años de aislamiento y ninguno ha monitoreado las condiciones por más de un año. Los datos microclimáticos presentados en el capítulo 4 representan un avance importante en esa dirección.

Contrario a lo que se esperaba, el sotobosque de los tres fragmentos estudiados presentaron un microclima semejante al observado en el sotobosque de la selva madura. Este patrón no fue sólo una fotografía en el tiempo, sino que se mantuvo constante por casi dos años. Tampoco fue producto de medidas tomadas lejos del borde de los fragmentos, porque éstas fueron tomadas generalmente en los primeros 100 m de la vegetación (además de pequeños [< 15 ha], los fragmentos eran irregulares). Una posible explicación puede ser que los cuerpos de agua y los parches de bosque secundario aledaños a los fragmentos redujeron las diferencias atmosféricas en ambos lados del borde y amenizaron los cambios microclimáticos dentro de los fragmentos (ver fenómeno conocido como "brisa de la vegetación" sensu Cochrane & Laurance 2008). También es probable que la sustitución de árboles de sucesión tardía por árboles de sucesión inicial, desencadenada por la creación del borde (Laurance et al. 2006, Santos et al. 2008, Tabarelli et al. 2008), redujo la estratificación de la selva y la altura del dosel, pero tras 25-35 años de fragmentación propició la estabilización del microclima a niveles pre-fragmentación. Un monitoreo reciente de la temperatura al nivel del suelo en la misma área de estudio registró una estabilidad microclimática semejante en fragmentos ocupados por monos aulladores que en selva contínua (González-Di Pierro et al. 2011). Fragmentos desocupados, sin embargo, presentaron un microclima dos grados más cálido que la selva continua, y la abertura de dosel (una medida indirecta de la incidencia de luz) fue menor en ambos tipos de fragmento que en la selva continua (González-Di Pierro et al. 2011). Esta heterogeneidad microclimática observada entre fragmentos de selva de una misma región indica que no se puede asumir que todos los fragmentos tienen un microclima alterado como se ha asumido frecuentemente en la literatura.

El nivel de conocimiento sobre la heterogeneidad microclimática de la matriz que rodea los fragmentos es aún menor, dado el sesgo actual de los estudios hacia los parches de vegetación original remanente (Kupfer et al. 2006 y referencias citadas). Se sabe que el nivel de heterogeneidad espacial en el microclima de la matriz es muy alto debido a la diferencia estructural entre sus diferentes componentes, pero observaciones empíricas son de hecho escasas; se espera un aumento en la temperatura y una reducción en la humedad relativa del aire debido a una mayor incidencia de luz en áreas deforestadas que en áreas boscosas (Chen et al. 1999, Laurance 2004). Esta predicción fue corroborada por el monitoreo microclimático realizado en los bordes de carretera y los claros naturales de la selva continua (ver también Delgado et al. 2007). Sin embargo, los claros en franjas estrechas de vegetación secundaria riparia degradada (< 50 m de ancho) presentaron un microclima semejante al observado en los claros naturales de la selva madura, lo que enfatiza el alto valor para la conservación de zonas riparias, aunque muy degradas (árboles grandes aislados en potreros tienen una relevancia similar; Williams-Linera et al. 1998).

No obstante, hubo por lo menos dos evidencias relacionadas a la abundancia de las plantas y sus enemigos naturales que sugieren una baja importancia de las condiciones microclimáticas en el establecimiento de las interacciones *Heliconia*-herbívoro y *Heliconia*-patógeno en la región de Chajul, ya sea dentro o fuera de los fragmentos. Primero, las heliconias características de sucesión temprana (*H. latispatha* y *H. collinsiana*) proliferaron tanto en hábitats con microclima semejante (zona riparia y claros naturales) como distinto (borde de carretera y claros naturales), probablemente debido a chapeos pasados (el chapeo induce el surgimiento de nuevos vástagos por propagación horizontal;

Berry & Kress 2001). Segundo, la abundancia de los tres grupos de herbívoros analizados − crisomélidos, orugas de Lepidoptera y hormigas cortadoras de hojas − tampoco varió consistentemente con las condiciones microclimáticas (e.g. las hormigas proliferaron y los crisomélidos declinaron en los fragmentos con respecto a la selva continua, independiente de la similitud microclimática entre ellos). Como resultado, los niveles totales de daño biótico tampoco variaron de acuerdo a las condiciones físicas. Por ejemplo, hábitats con microclima similar presentaron una reducción en el daño total por insectos (*H. collinsiana* en zonas riparias y claros naturales), así como un aumento de daños por patógenos (*H. aurantiaca* en fragmentos de selva y selva continua). No obstante, hay que considerar que las condiciones microclimáticas no fueron registradas a nivel de las hojas (i.e. filosfera) de las especies de heliconia estudiadas, sino que a 1.3 m por encima del suelo.

Calidad/disponibilidad de plantas hospederas y daño biótico

La calidad de la planta hospedera puede afectar el crecimiento y la fecundidad de insectos herbívoros y hongos patógenos y por lo tanto influenciar las interacciones de estos organismos con sus plantas hospederas (Awmack & Leather 2002, Agrios 2005). Similarmente, la disponibilidad de hospederos por unidad de área también puede determinar la incidencia y la magnitud de los daños bióticos (Burdon & Chilvers 1982, Coley & Barone 1996, Gilbert 2002). La hipótesis de Janzen-Connell, ampliamente reconocida como uno de los mecanismos de mantenimiento de diversidad biológica en selvas tropicales (Janzen 1970, Connell 1971, Wright 2002), está fundamentada precisamente en cambios espaciales en la disponibilidad local de hospederos. Los datos de las heliconias de Chajul, sin embargo, sugieren que a ejemplo de las condiciones microclimáticas, la calidad y la disponibilidad de hospederos no son buenos predictores de daños foliares (ver Benítez-Malvido et al. 2005 y Fáveri et al. 2008 para un patrón similar en la Amazonia Brasileña).

Una posible explicación para ello es que el aumento promedio en la dureza foliar causado por el hombre (41-84 g/cm^2) fue menor que la variación natural observada entre las especies de heliconias estudiadas (96 g/cm^2), las cuales son consumidas por el mismo ensamble de herbívoros en condiciones naturales (Strong 1977a, b; Auerbach and Strong 1981, DeVries 1987). Además, aunque la perturbación humana haya resultado en un aumento en los niveles de defensa física de las heliconias de *H. latispatha* y *H. collinsiana* (la dureza foliar parece ser el principal mecanismo de defensa de las heliconias; Gage & Strong 1981, Dominy et al. 2008), este incremento resultó en una reducción en los niveles totales de daño sólo en *H. collinsiana*. Al menos con base en esos datos, no es posible afirmar que la herbivoría por insectos en hábitats alterados es mayormente mediada por cambios en la calidad del hospedero.

Los cambios en la disponibilidad local de plantas hospederas tampoco tuvieron un efecto claro sobre las interacciones estudiadas. En los bordes de carretera y zonas riparias, hubo un aumento en la densidad local de vástagos y una tendencia de aumento en los niveles de daño por patógenos, lo que sugiere una correlación positiva entre disponibilidad de hospederos y niveles de daño como predicho por la hipótesis de Janzen-Connell. En los fragmentos de selva también se observó un aumento en los niveles de daños por patógenos en comparación a la selva continua, pero dicho aumento se dio incluso cuando las plantas estaban sujetas a densidades similares. Esto sugiere que la proliferación de enfermedades en selvas tropicales fragmentadas se puede dar también sin un incremento evidente en la disponibilidad de hospederos, lo que todavía no se había reportado. Estudios futuros podrían manipular experimentalmente la densidad de vástagos en condiciones naturales para identificar umbrales por encima de los cuales los daños por patógenos aumentan.

Abundancia de herbívoros y daño biótico

Al contrario de las condiciones microclimáticas y de la calidad y disponibilidad de hospederos, los cambios en la abundancia local de los insectos herbívoros fueron siempre consistentes con aquellos en los daños foliares. En hábitats donde un determinado herbívoro abundabó, su daño relativo fue mayor, y vice versa. Esta relación, obvia en cierto sentido, se observó tanto en los hábitats control (claros naturales y sotobosque de la selva continua) como en los fragmentos de selva y hábitats alterados de la matriz. Estos resultados indican que la capacidad de predecir daños foliares en selvas fragmentadas pasa necesariamente por el entendimiento de las fuerzas que determinan la abundancia y distribución de los herbívoros. Aunque los factores que regulan las poblaciones de herbívoros no fueron objeto de estudio de esta tesis, la contextualización de sus resultados con otros estudios permite inferir los posibles mecanismos que han llevado a la proliferación de unas especies de herbívoros y a la disminución de otras especies en la región de Chajul.

Las poblaciones de herbívoros pueden ser reguladas por las condiciones ambientales, calidad y disponibilidad de plantas palatables (control ascendiente), depredadores y parasitoides (control descendente), y también por la habilidad del insecto de dispersarse por el paisaje (e.g. Fáveri et al. 2008, Wirth et al. 2008, Ruiz-Guerra et al. 2010). Como demostrado anteriormente, la abundancia local de los diferentes herbívoros − y los daños que ellos causaron − no variaron consistentemente ni con las condiciones ambientales ni con la calidad y disponibilidad de los hospederos, lo que sugiere un papel secundario de estas fuerzas en la determinación de la abundancia de insectos folívoros en el sistema estudiado. La capacidad de dispersión parecía ser importante dado el aislamiento generado por la deforestación y fragmentación, pero el hecho de que los tres grupos de herbívoros fueron encontrados en los cinco hábitats considerados sugiere que los insectos folívoros de las heliconias, aunque diferentes en términos de tamaño, capacidad de vuelo, y amplitud de dieta, pueden dispersarse por todo el paisaje modificado.

La explicación más plausible para las diferencias observadas en la abundancia de insectos parece estar asociada con los cambios positivos y negativos en el control descendente de las poblaciones de los insectos. Existe evidencia de que los fragmentos de selva pierden depredadores y parasitoides, resultando en la "liberación ecológica" de las presas, de las cuales muchas son herbívoros (e.g. Stouffer & Bierregaard 1995, Kruess & Tscharntke 2000, Rao 2000, Terborgh et al. 2001, Şekercioḡlu et al. 2002). Como consecuencia del relajamiento del control descendente de los herbívoros, las redes tróficas son simplificadas, las comunidades biológicas se empobrecen, y los flujos de materia y energía se alteran (Wirth et al. 2008). La proliferación de hormigas cortadoras de hojas en fragmentos de selva ilustran muy bien este proceso de deterioro del ecosistema que puede ser inducido por la pérdida de depredadores y parasitoides (Terborgh et al. 2001, Almeida et al. 2008; las hormigas cortadoras también se favorecen del relajamiento del control ascendiente [Urbas et al. 2007]). Un proceso semejante parece estar sucediendo en la región de Chajul, ya que se observaron seis veces más colonias de estos insectos sociales en los fragmentos de selva que en la selva continua.

Menos popular pero igualmente fundamentada en datos empíricos está otra corriente que defiende que en vez de disminuir, el control descendente aumenta tras la perturbación humana (e.g. Vergara & Simonetti 2004, González-Gómez et al. 2006, Valladares et al.

2006, Simonetti et al. 2007, Lluch et al. 2009). Una de las premisas de esta hipótesis es que los depredadores y parasitoides no son ecológicamente equivalentes, y que así como algunas plantas y herbívoros, también hay depredadores y parasitoides que se pueden favorecer en hábitats alterados o manejados (e.g. Strong 1984). Una predicción de la hipótesis de aumento del control descendente en hábitats alterados es la disminución de la abundancia de presas (e.g. herbívoros) en estos hábitats en comparación al hábitat no alterado. Eso fue precisamente lo que se observó con los crisomélidos en los fragmentos de selva y con las orugas de Lepidoptera en el borde de carretera y zonas riparias alteradas de la región de Chajul: ambos sufrieron una reducción drástica en términos de abundancia local. En resumen, los resultados sugieren una disminución en el control descendente de las hormigas cortadoras y un aumento en el control descendente de los crisomélidos y orugas en hábitats alterados, por lo que apoya a las dos corrientes divergentes que alimentan la actual controversia sobre el tema. Más estudios son necesarios para entender cómo el control descendente regula las poblaciones de herbívoros en selvas fragmentadas (Wirth et al. 2008).

Daño biótico y desempeño de la planta hospedera

El desempeño de las plantas tras el ataque de herbívoros y patógenos depende principalmente de la estrategia de defensa adoptada después del daño. Las plantas utilizan dos grandes estrategias de defensa contra sus enemigos naturales: la resistencia y la tolerancia al daño. La resistencia puede ser definida como cualquier respuesta constitutiva o inducida de la planta contra los herbívoros para evitar o disminuir la cantidad de daño, mientras que la tolerancia es una respuesta de la planta, inducida por el daño, para reducir los efectos negativos del daño sobre su desempeño (Núñez-Farfán et al. 2007; ver también

Strauss & Agrawal 1999, Strauss et al. 2002, Kessler & Baldwin 2002). Las dos estrategias son heredables y parecen evolucionar simultáneamente bajo un proceso en el cual los niveles intermediarios de tolerancia y resistencia son favorecidos ("patrón mixto de asignación de defensa" sensu Núñez-Farfán et al. 2007; pero ver Stowe et al. 2000 y referencias citadas para ejemplos sobre evolución antagonista entre tolerancia y resistencia).

Mientras los mecanismos evolutivos que dan origen a las dos estrategias de defensa siguen siendo discutidos, lo que generalmente se observa en selvas altas perennifolias es que las plantas de crecimiento rápido, típicas de claros naturales, reúnen muchos atributos asociados con alta tolerancia al daño biótico, mientras que aquellas de crecimiento lento, típicas del sotobosque de la selva, tienen más características asociadas con alta resistencia (Coley et al. 1985, Coley & Barone 1996; ver también Stamp 2003). Las pioneras de crecimiento rápido no sufren limitación de luz en los claros naturales, por lo que pueden producir más estructuras vegetativas y reproductivas de lo que les dañan los herbívoros (alta tolerancia). En lugar de invertir en defensas constitutivas o inducidas que reduzcan la preferencia o el desempeño del herbívoro, las plantas pioneras compensan el daño a través de un rápido crecimiento y producción frecuente y copiosa de propágulos. Los individuos de *H. latispatha* y *H. collinsiana* son ejemplos de este grupo de especies pioneras tolerantes a la herbivoría. Al contrario de las pioneras, las especies de sucesión tardía que se han adaptado a las condiciones de sombra del sotobosque tienen su crecimiento limitado por la baja disponibilidad de recursos, por lo que tienen baja capacidad para compensar el daño causado por los herbívoros (alta resistencia). Para estas plantas la mejor estrategia es evitar ser consumida o asegurar niveles muy bajos de consumo a través de la producción de un sin número de defensas químicas y físicas.

El hecho de que *H. aurantiaca* habita el sotobosque la pondría en este grupo de especies resistentes a la herbivoría, pero en realidad la especie presenta, así como las demás del género *Heliconia*, una serie de atributos asociados con alta tolerancia a la herbivoría. Si bien *H. aurantiaca* produce hojas e inflorescencias muy pequeñas y un bajo número de flores y semillas en relación a las heliconias pioneras, comparada a la gran mayoría de los árboles y arbustos que habitan el sotobosque, tiene hojas menos longevas, mayores tasas de crecimiento[3], reproducción más frecuente (anual) y mayor relación raíz:tallo (su equivalente ecológico en el Amazonas, *H. acuminata*, concentra hasta el 85% de su biomasa en el rizoma; Bruna et al. 2002, Bruna & Ribeiro 2005). Estas características sugieren que *H. aurantiaca* es tolerante a la herbivoría aunque habite el sotobosque de la selva. Además, los resultados presentados en capítulo 4 demuestran que en condiciones naturales no hay una correlación entre el nivel de daño foliar y el desempeño de la planta, lo que también sugiere alta tolerancia. Sin embargo, cabe mencionar que para evaluar adecuadamente la habilidad de esta especie para compensar los daños foliares, se requiere un abordaje experimental en el cual un mismo genotipo sea sometido a diferentes niveles de daño (ver Strauss & Agrawal 1999).

Implicaciones para el manejo de *Heliconia* en selvas secundarias y degradadas

La región de Chajul cuenta con ocho especies nativas de *Heliconia* que varían en tamaño (0.5–5.0 m), hábito de crecimiento (musoide, zingiberoide o canoide), orientación de la inflorescencia (erecta o pendiente), disposición de las brácteas (dísticas o en espiral), color

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[3] En ocho meses los vástagos recién germinados ya están listos para reproducirse (ver capitulo 4), mientras que las plántulas de muchos árboles de crecimiento lento generalmente crecen unos pocos centímetros.

de las brácteas (distintos tonos de rojo, naranja y amarillo) y período de floración (a cualquier momento del año hay por lo menos dos especies en floración). La mayoría de las especies son pioneras típicas de estadios iniciales de sucesión, por lo que abundan en los hábitats alterados de la región, y ya están bien establecidas en el mercado internacional de plantas ornamentales (e.g. *H. wagneriana*, *H. latispatha, H. collinsiana*). Para algunas de ellas existe incluso información técnica sobre su cosecha, procesamiento y transporte (e.g. Hansen et al. 1992, Loges et al. 2005). Las plagas y enfermedades registradas para *Heliconia* atacan principalmente sus hojas, que no es el recurso económico más valioso de la planta; la inflorescencia es lo más importante y sólo el 16% de las especies de herbívoros y patógenos reportadas hasta el momento atacan esta parte de la planta. Todas las especies del género, incluyendo a aquellas que se han adaptado al sotobosque sombreado, parecen tener una alta capacidad para tolerar los daños foliares y reproducirse adecuadamente en presencia de sus enemigos naturales.

En conjunto, estas características revelan un alto potencial para el aprovechamiento de las heliconias nativas de la región de Chajul. Los bosques secundarios, campos abandonados y fragmentos de vegetación original podrían ser “enriquecidos” con las heliconias para aumentar el valor económico de estas áreas “improductivas” y los ingresos para la comunidad local. En los fragmentos se podrían utilizar los claros naturales para el cultivo de *H. latispatha*, *H. collinsiana*, y *H. wagneriana*, mientras que el sotobosque podría ser usado para el cultivo de *H. aurantiaca* y *H. librata*. El control de la mayoría de los herbívoros se podría hacer manualmente o con ayuda de redes entomológicas (Assis et al. 2002). El control de los patógenos sería más difícil sin el uso de fungicidas y probablemente requeriría el desarrollo de nuevas técnicas. Sin embargo, algunas medidas preventivas como utilizar herramientas limpias y sembrar las plantas en suelos estériles y bien drenados antes del trasplante al agroecosistema podrían reducir las pérdidas causadas por patógenos (ver Sewake & Uchida 1995, Assis et al. 2002). Localmente, también se podría incentivar el uso de las hojas como substituto para las hojas de plátanos. Una de las especies de Chajul, *H. champneiana*, que incluso parece ser la más rara en la región junto con *H. spissa*, tiene hojas con más de dos metros de largo muy semejantes a las hojas de plátano. *H. collinsiana*, otra de las especies con hojas muy grandes, probablemente no tendría la misma utilidad debido a la gran cantidad de cera pulverulenta blanca que se encuentra en el envés de sus hojas.

En suma, las heliconias son un recurso poco utilizado en la región de Chajul y tienen potencial para constituir un importante instrumento de conservación en la Selva Lacandona. Es muy probable que otras regiones del Sureste de México tengan un potencial parecido, ya que ninguna de las ocho especies reportadas para Chajul es endémica (todas deben ocurrir naturalmente en gran parte de La Lacandona). Las selvas altas fragmentadas de la región de Los Tuxtlas, Veracruz, también cuentan con por lo menos tres especies de heliconias nativas (*H. latispatha*, *H. librata*, y la endémica *H. uxpanapensis*; B. A. Santos, observación personal), pero que son igualmente sub-utilizadas del punto de vista ornamental. Se espera que esta tesis pueda tener alguna utilidad para la formulación de políticas públicas que combinen desarrollo social y económico con conservación biológica en las selvas altas perennifolias del país.

CONCLUSIONES GENERALES

1. La perturbación humana beneficia a los herbívoros generalistas en detrimento de los especialistas y favorece la proliferación de enfermedades foliares en el área de estudio;

2. La proliferación de herbívoros generalistas en los hábitats alterados estudiados no siempre resulta en un aumento en el nivel total de daño foliar, ni en la subsecuente reducción en el desempeño de la planta hospedera;

3. Aunque las condiciones físicas, la calidad y la disponibilidad de plantas hospederas puedan afectar los niveles de herbivoría, el factor ecológico más importante en este proceso parece ser la abundancia local de herbívoros;

4. Hay un alto potencial para el aprovechamiento de heliconias nativas en las selvas secundarias y degradadas de la región de Chajul, Chiapas, y probablemente en otras regiones tropicales de la república mexicana.

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