

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

Bráulio A. Santos<sup>1</sup> and Julieta Benítez-Malvido

Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México (UNAM), Antigua Carretera a Pátzcuaro No. 8701, Ex Hacienda de San José de la Huerta, 58190 Morelia, Michoacán, Mexico

### 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).

Received 31 August 2010; revision accepted 8 December 2010.

<sup>1</sup>Corresponding author; e-mail: bsantos@oikos.unam.mx

© 2011 The Author(s)

Journal compilation © 2011 by The Association for Tropical Biology and Conservation

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-1970s. 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<sup>2</sup>), naturally formed young gaps embedded in a 3.5 km<sup>2</sup> 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<sup>®</sup> 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  $\pm 0.35^\circ\text{C}$  for temperature and  $\pm 2.5$  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<sup>®</sup> 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  $\text{g}/\text{cm}^2$ ). 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 ( $7.2\% \pm 1.0\%$ ; mean  $\pm$  SE) and road edges ( $8.0\% \pm 3.4\%$ ) ( $F_{1,18} = 0.02$ ;  $P = 0.884$ ). 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 ( $3.0\% \pm 1.1\%$  vs.  $6.7\% \pm 1.8\%$ ) ( $F_{1,18} = 3.79$ ;  $P = 0.067$ ). 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  $6.2 \pm 1.8$  percent in forest gaps to  $2.5 \pm 1.0$  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.

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 ( $8.2\% \pm 2.4\%$  vs.  $4.2\% \pm 1.0\%$ ; 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 ( $9.6\% \pm 4.1\%$  vs.  $3.7\% \pm 1.9\%$ ; 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*  $\times$  *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

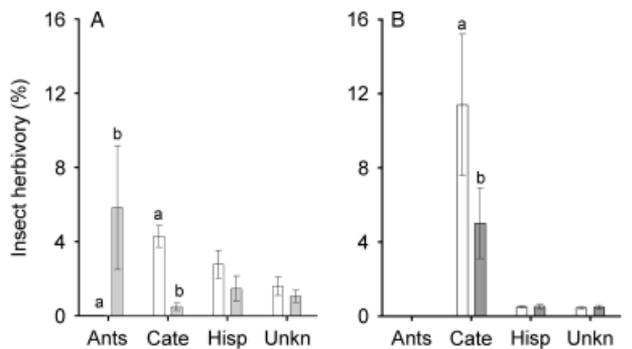


FIGURE 1. Standing levels of foliar damage (mean  $\pm$  SE) by leaf-cutting ants (Ants), caterpillars (Cate), hispine beetles (Hisp), and unknown insects (Unkn) on the foliage of (A) *Heliconia latispatha* and (B) *Heliconia collinsiana* in forest gaps (white bars), road edges (lightly shaded bars), 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,  $P < 0.05$ ).

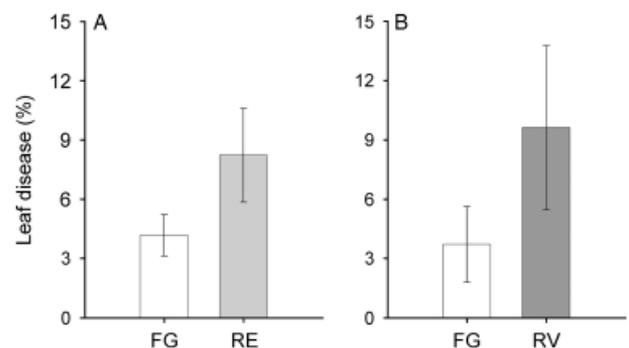


FIGURE 2. Standing levels of pathogen damage (mean  $\pm$  SE) on the foliage of (A) *Heliconia latispatha* and (B) *Heliconia collinsiana* in forest gaps (FG), road edges (RE), and secondary riparian vegetation (RV) in the region of Chajul, southern Mexico.

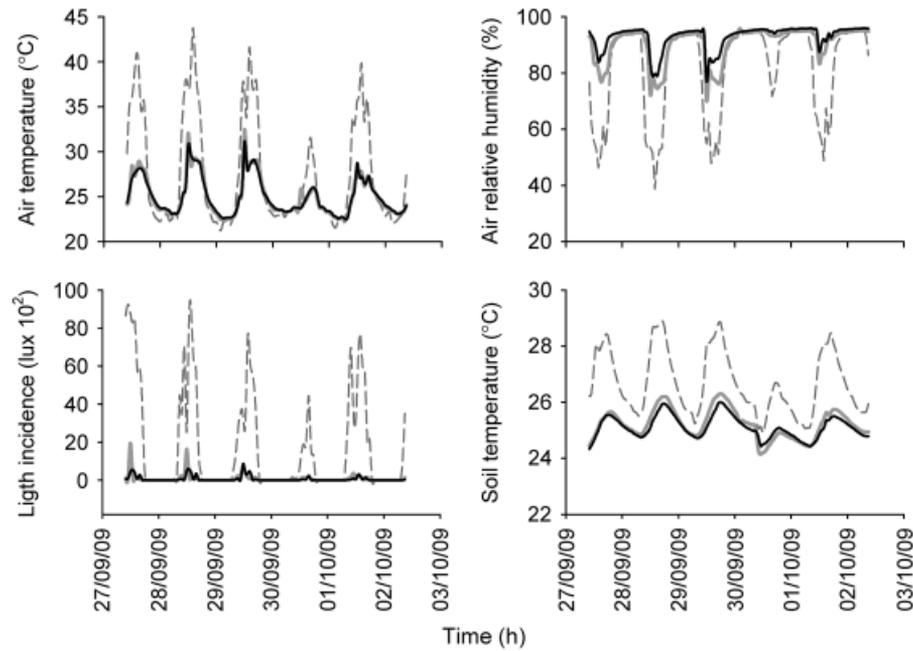


FIGURE 3. Daily patterns of air temperature, air relative humidity, light incidence, and soil temperature in forest gaps (black solid line), road edges (dashed line), secondary riparian vegetation (gray solid line) in the region of Chajul, southern Mexico. Recording started on 27 September 2009 at 1000 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, southern Mexico.

Model terms	df	F-ratio	P-value	Model $R^2$
<b>Air temperature</b>				
Habitat	2,3	4.52	0.124	0.90
Time	119,357	18.00	< 0.0001	
Habitat $\times$ time	238,357	3.30	< 0.0001	
<b>Air relative humidity</b>				
Habitat	2,3	8.47	0.058	0.93
Time	119,357	23.27	< 0.0001	
Habitat $\times$ time	238,357	4.48	< 0.0001	
<b>Light incidence</b>				
Habitat	2,3	13.02	0.033	0.94
Time	119,357	31.20	< 0.0001	
Habitat $\times$ time	238,357	3.56	< 0.0001	
<b>Soil temperature</b>				
Habitat	2,3	3.86	0.148	0.85
Time	119,357	5.13	< 0.0001	
Habitat $\times$ 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 ( $1.7 \pm 0.6$  vs.  $0.3 \pm 0.2$  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 ( $2.7 \pm 0.7$  vs.  $0.9 \pm 0.3$  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

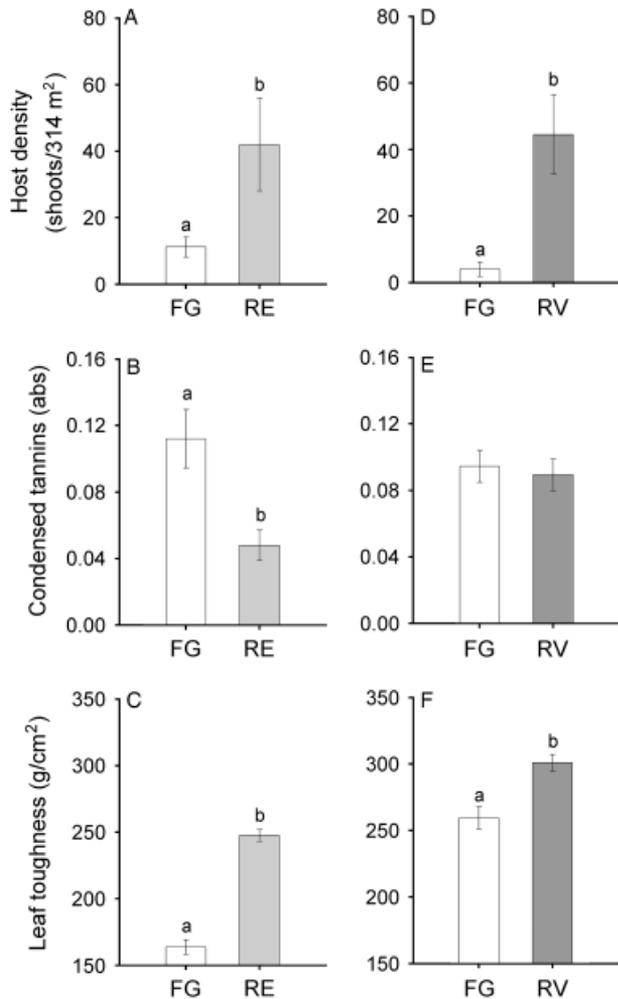


FIGURE 4. Host density, absorbance of foliar condensed tannins and leaf toughness (mean  $\pm$  SE) of *Heliconia latispatha* (A–C) and *Heliconia collinsiana* (D–F) in forest gaps (FG), road edges (RE), and secondary riparian vegetation (RV) in the region of Chajul, southern Mexico. Different letters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

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

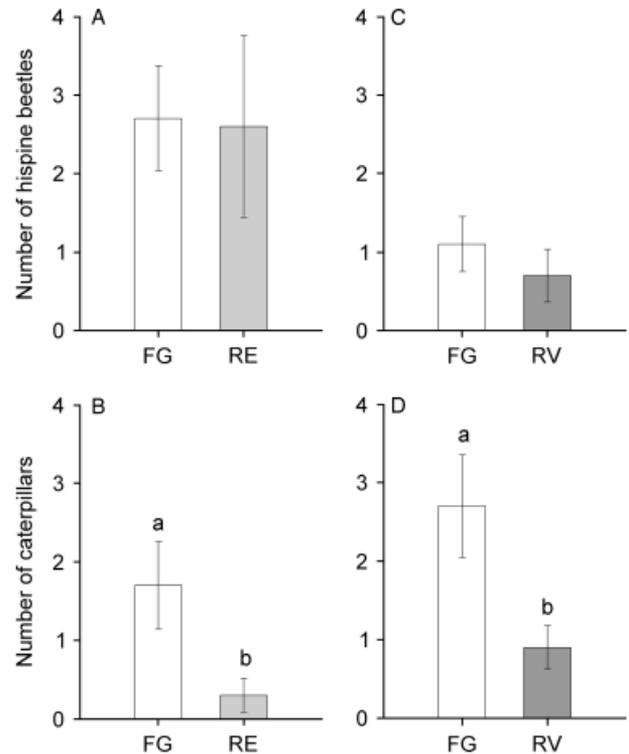


FIGURE 5. Local abundance of hispine beetles and caterpillars (mean  $\pm$  SE) on the foliage of *Heliconia latispatha* (A–B) and *Heliconia collinsiana* (C–D) in forest gaps (FG), secondary riparian vegetation (RV), and road edges (RE) in the region of Chajul, southern Mexico. Different letters indicate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

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, 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 plau-

sible explanation for the decrease in caterpillar damage we observed. The magnitude of the human-induced increase in leaf toughness (41–84 g/cm<sup>2</sup>), however, was smaller than the difference naturally observed between the *Heliconia* species examined (96 g/cm<sup>2</sup>), 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.

## ACKNOWLEDGMENTS

We are extremely grateful to Mauricio Quesada and Francisco Espinosa for valuable suggestions and discussions during the development of this study; Rafael Lombera and Eva Stadler for field and laboratory assistance; Ek del Val, Karina Boege, and Roberto Cisneros for research facilities and technical support; and Donald Strong, Julian Norghauer, and an anonymous reviewer for helpful comments on previous versions of this manuscript. We appreciate essential financial and logistic support from Universidad Nacional Autónoma de México (Project Papiit IN220008 to JBM), Consejo Nacional de Ciencia y Tecnología de México (Project 2007-C01-79121, graduate scholarship to BAS and research grant to JBM), and Rufford Small Grants Foundation (RSG 40.08.08 to BAS). This paper constitutes a partial fulfillment of the Graduate Program in Biological Sciences of the Universidad Nacional Autónoma de México.

## 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.

Please note: Wiley-Blackwell is not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

## LITERATURE CITED

- AGRIOS, G. N. 2005. Plant pathology (5th edition). Elsevier Academic Press, London, U.K.
- ALMEIDA, W. R., R. WIRTH, AND I. R. LEAL. 2008. Edge-mediated reduction of phorid parasitism on leaf-cutting ants in a Brazilian Atlantic forest. *Entomol. Exp. Appl.* 129: 251–257.
- ASSIS, S. M. P., R. R. L. MARIANO, M. G. C. GONDIM JR., M. MENEZES, AND R. C. T. ROSA. 2002. Diseases and pests of *Heliconia*—Doenças e pragas das *Helicônias*. Editora da UFRPE, Recife, Brazil.
- AUERBACH, M. J., AND D. R. STRONG. 1981. Nutritional ecology of *Heliconia* herbivores: Experiments with plant fertilization and alternative hosts. *Ecol. Monogr.* 51: 63–83.
- AWMACK, C. S., AND S. R. LEATHER. 2002. Host plant quality and fecundity in herbivorous insects. *Annu. Rev. Entomol.* 47: 817–844.
- BENÍTEZ-MALVIDO, J., AND A. LEMUS-ALBOR. 2005. The seedling community of tropical rain forest edges and interactions with herbivores and leaf-pathogens. *Biotropica* 37: 301–313.
- BENÍTEZ-MALVIDO, J., AND A. LEMUS-ALBOR. 2006. Habitat disturbance and the proliferation of plant diseases. In W. F. Laurance and C. A. Peres (Eds.). *Emerging threats to tropical forests*, pp. 165–174. University of Chicago Press, Chicago, Illinois.
- BERRY, F., AND W. J. KRESS. 1991. *Heliconia: An identification guide*. Smithsonian Institution Press, Washington, DC.
- BOEGE, K. 2005. Herbivore attack in *Casearia nitida* influenced by plant ontogenetic variation in foliage quality and plant architecture. *Oecologia* 143: 117–125.
- BROKAW, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66: 682–687.
- BURDON, J. J. 1993. The structure of pathogen populations in natural plant communities. *Annu. Rev. Phytopathol.* 31: 305–323.
- BURDON, J. J., P. H. THRALL, AND L. ERICSON. 2006. The Current and future dynamics of disease in plant communities. *Annu. Rev. Phytopathol.* 44: 1.1–1.21.
- CAMARGO, J. L. C., AND V. KAPOS. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. *J. Trop. Ecol.* 11: 205–211.
- COLEY, P. D., AND J. A. BARONE. 1996. Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27: 305–335.
- CUARÓN, A. D. 2000. A global perspective on habitat disturbance and tropical rainforest mammals. *Conserv. Biol.* 14: 1574–1579.
- DELGADO, J. D., N. L. ARROYO, J. R. ARÉVALO, AND J. M. FERNÁNDEZ-PALACIOS. 2007. Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). *Landscape Urban Plann.* 81: 328–340.
- DE VRIES, P. J. 1987. The butterflies of Costa Rica and their natural history—Volume 1: Papilionidae, Pieridae, and Nymphalidae. Princeton University Press, Princeton, New Jersey.
- DIDHAM, R. K., AND J. H. LAWTON. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31: 17–30.
- DOMINY, N. J., P. J. GRUBB, R. V. JACKSON, P. W. LUCAS, D. J. METCALFE, J. C. SVENNING, AND I. M. TURNER. 2008. In tropical lowland rain forests monocots have tougher leaves than dicots, and include a new kind of tough leaf. *Ann. Bot.* 101: 1363–1377.
- DYER, L. A., R. B. MATLOCK, D. CHEHREZAD, AND R. O'MALLEY. 2005. Predicting caterpillar parasitism in banana plantations. *Environ. Entomol.* 34: 403–409.
- FÁVERI, S. B., H. L. VASCONCELOS, AND R. DIRZO. 2008. Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. *J. Trop. Ecol.* 24: 57–64.
- FIGUEROA, F., V. SÁNCHEZ-CORDERO, J. A. MEAVE, AND I. TREJO. 2009. Socio-economic context of land use and land cover change in Mexican biosphere reserves. *Environ. Conserv.* 36: 180–191.
- FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS. 2009. State of the world's forest 2009. FAO, Rome, Italy.
- GAGE, D. A., AND D. R. STRONG. 1981. The chemistry of *Heliconia imbricata* and *H. latspatha* and the slow growth of a hispine beetle herbivore. *Biochem. Syst. Ecol.* 9: 79–82.
- GARCÍA-GUZMÁN, G., AND R. DIRZO. 2001. Pattern of leaf-pathogen infection in the understory of a Mexican rain forest: Incidence, spatiotemporal variation, and mechanisms of infection. *Am. J. Bot.* 88: 634–645.
- GARCÍA-GUZMÁN, G., AND R. DIRZO. 2004. Incidence of leaf pathogens in the canopy of a Mexican tropical wet forest. *Plant Ecol.* 172: 41–50.
- GARDNER, T. A., J. BARLOW, R. CHAZDON, R. M. EWERS, C. A. HARVEY, C. A. PERES, AND N. S. SODHI. 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecol. Lett.* 12: 561–582.
- GILBERT, G. S. 2002. Evolutionary ecology of plant diseases in natural ecosystems. *Annu. Rev. Phytopathol.* 40: 13–43.
- GILBERT, G. S., AND S. P. HUBBELL. 1996. Plant diseases and the conservation of tropical forests. *Bioscience* 46: 98–106.
- HARPER, K. A., S. E. MACDONALD, P. J. BURTON, J. CHEN, K. D. BROSOFSKE, S. C. SAUNDERS, E. S. EUSKIRCHEN, D. ROBERTS, M. S. JAITEH, AND P. ESSEEN. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conserv. Biol.* 19: 768–782.
- HENNEN, J. F., M. B. FIGUEIREDO, A. A. CARVALHO, AND F. G. HENNEN. 2005. Catalogue of the species of plant rust fungi (Uredinales) of Brazil. FAPESP, CNPq, FAPERJ, NSF, and USDA, São Paulo, Brazil.
- KAPOS, V., G. GANADE, E. MATSUI, AND R. L. VICTORIA. 1993.  $\delta^{13}C$  as an indicator of edge effects in tropical rainforest reserves. *J. Ecol.* 81: 425–432.
- LAMARI, L. 2002. Assess: Image analysis software for plant disease quantification. The American Phytopathological Society, Winnipeg, Canada.
- LAURANCE, W. F. 2005. The alteration of biotic interactions in fragmented tropical forests. In D. F. R. P. Burslem, M. A. Pinard, and S. E. Hartley (Eds.). *Biotic interactions in the tropics: Their role in the maintenance of species diversity*, pp. 441–458. Cambridge University Press, Cambridge, U.K.
- LAURANCE, W. F., AND R. O. BIERREGAARD JR. 1997. Tropical forest remnants: Ecology, management, and conservation of fragmented communities. University of Chicago Press, Chicago, Illinois.
- LAURANCE, W. F., M. GOOSEM, AND S. G. LAURANCE. 2009. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol.* 24: 659–669.
- LAURANCE, W. F., T. E. LOVEJOY, H. L. VASCONCELOS, E. M. BRUNA, R. K. DIDHAM, P. C. STOFFER, C. GASCON, R. O. BIERREGAARD, S. G. LAURANCE, AND E. SAMPAIO. 2002. Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conserv. Biol.* 16: 605–618.
- LAURANCE, W. F., AND C. A. PERES. 2006. Emerging threats to tropical forests. University of Chicago Press, Chicago, Illinois.

- LINS, S. R. O., AND R. S. B. COELHO. 2004. Ocorrência de Doenças em Plantas Ornamentais Tropicais no Estado de Pernambuco. *Fitopatol. Bras.* 29: 332–335.
- LUGO, A. E. 2009. The emerging era of novel tropical forests. *Biotropica* 41: 589–591.
- MALCOLM, J. R. 1994. Edge effects in central Amazonian forest fragments. *Ecology* 75: 2438–2445.
- MARQUIS, R. J. 2005. Impacts of herbivores on tropical plant diversity. In D. F. R. P. Burslem, M. A. Pinar, and S. E. Hartley (Eds.), *Biotic interactions in the tropics: Their role in the maintenance of species diversity*, pp. 328–346. Cambridge University Press, Cambridge, U.K.
- MEYER, S. T., I. R. LEAL, AND R. WIRTH. 2009. Persisting hyper-abundance of leaf-cutting ants (*Atta* spp.) at the edge of an old Atlantic forest fragment. *Biotropica* 41: 711–716.
- MURCIA, C. 1995. Edge effects in fragmented forests: Implications for conservation. *Trends Ecol. Evol.* 10: 58–62.
- MYERS, N., R. A. MITTERMEIER, C. G. MITTERMEIER, G. A. B. FONSECA, AND J. KENT. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- NEWMARK, W. D. 2001. Tanzanian forest edge microclimatic gradients: Dynamic patterns. *Biotropica* 33: 2–11.
- POHLMAN, C. L., S. M. TURTON, AND M. GOOSEM. 2007. Edge effects of linear canopy openings on tropical rain forest understory microclimate. *Biotropica* 39: 62–71.
- POTVIN, C. 2001. Anova: Experimental layout and analysis. In S. M. Scheiner and J. Gurevitch (Eds.), *Design and analyses of experimental ecological experiments*, pp. 63–76. Oxford University Press, Oxford, U.K.
- RICO-GRAY, V., AND P. S. OLIVEIRA. 2007. *The ecology and evolution of ant-plant interactions*. University of Chicago Press, Chicago, Illinois.
- SANTOS, B. A., R. LOMBERA, AND J. BENÍTEZ-MALVIDO. 2009. New records of *Heliconia* (Heliconiaceae) for the region of Chajul, Southern Mexico, and their potential use in biodiversity-friendly cropping systems. *Rev. Mex. Biod.* 80: 857–860.
- SCHNITZER, S. A., AND W. P. CARSON. 2001. Treefall gaps and the maintenance of species diversity in a tropical forest. *Ecology* 82: 913–919.
- SEIFERT, R. P. 1982. Neotropical *Heliconia* insect communities. *Q. Rev. Biol.* 57: 1–28.
- SERRA, I. M. R. S., AND R. S. B. COELHO. 2007. Mancha de *Pestalotiopsis* em helicônia: Caracterização da doença e potenciais fontes de resistência. *Fitopatol. Bras.* 32: 44–49.
- SEWAKE, K. T., AND J. Y. UCHIDA. 1995. *Diseases of Heliconia in Hawaii*. Research extension series 159. Hawaii Institute of Tropical Agriculture and Human Resources, Honolulu, Hawaii.
- SIEBE, C., M. MARTÍNEZ-RAMOS, G. SEGURA-WARNHOLTZ, J. RODRÍGUEZ-VELÁZQUEZ, AND S. SÁNCHEZ-BELTRÁN. 1995. Soils and vegetation patterns in the tropical rainforest at Chajul, Southeast Mexico. In D. Simorangkir (Ed.), *Proceedings of the international congress on soils of tropical forest ecosystems. 3rd conference on forest soils (ISSS-AISS-IBG)*, pp. 40–58. Mulwarman University Press, Samarinda, Indonesia.
- STILES, F. G. 1975. Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology* 56: 285–301.
- STRONG, D. R. 1977a. Rolled-leaf hispine beetles (Chrysomelidae) and their Zingiberales host plants in Middle America. *Biotropica* 9: 156–169.
- STRONG, D. R. 1977b. Insect species richness: Hispine beetles of *Heliconia latispatha*. *Ecology* 58: 573–582.
- TERBORGH, J., L. LOPEZ, V. P. NUÑEZ, M. RAO, G. SHAHABUDDIN, G. ORIHUELA, M. RIVEROS, R. ASCANIO, G. H. ADLER, T. D. LAMBERT, AND L. BALBAS. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294: 1923–1926.
- UHL, C. 1982. Recovery following disturbances of different intensities in the Amazon rain forest of Venezuela. *Interciencia* 7: 19–24.
- VASCONCELOS, H. L., E. H. M. VIEIRA-NETO, F. M. MUNDIM, AND E. M. BRUNA. 2006. Roads alter the colonization dynamics of a keystone herbivore in neotropical savannas. *Biotropica* 38: 661–665.
- VON ENDE, C. N. 2001. Repeated-measures analyses: Growth and other time-dependent measures. In S. M. Scheiner and J. Gurevitch (Eds.), *Design and analyses of experimental ecological experiments*, pp. 134–157. Oxford University Press, Oxford, U.K.
- WATANABE, M. A. 2007. Pragas da bananeira atacando *Heliconia latispatha* Benth. (Heliconiaceae). *Neotrop. Entomol.* 36: 312–313.
- WATERMAN, P. G., AND S. MOLE. 1994. *Analysis of phenolic plant metabolites*. Blackwell Scientific Publications, Oxford, U.K.
- WILF, P., C. C. LABANDEIRA, W. J. KRESS, C. L. STAINES, D. M. WINDSOR, A. L. ALLEN, AND K. R. JOHNSON. 2000. Timing the radiations of leaf beetles: Hispines on gingers from latest cretaceous to recent. *Science* 289: 291–294.
- WILLIAMS-LINERA, G. 1990. Vegetation structure and environmental conditions of forest edges in Panama. *J. Ecol.* 78: 356–373.
- WILLIAMS-LINERA, G., V. DOMÍNGUEZ-GASTELÚ, AND M. E. GARCÍA-ZURITA. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conserv. Biol.* 12: 1091–1102.
- WIRTH, R., S. T. MEYER, W. R. ALMEIDA, M. V. ARAÚJO, V. S. BARBOSA, AND I. R. LEAL. 2007. Increasing densities of leaf-cutting ants (*Atta* spp.) with proximity to the edge in a Brazilian Atlantic forest. *J. Trop. Ecol.* 23: 501–505.
- WIRTH, R., S. T. MEYER, I. R. LEAL, AND M. TABARELLI. 2008. Plant-herbivore interactions at the forest edge. *Prog. Bot.* 69: 423–448.
- WHITMORE, T. C. 1989. Canopy gaps and two major groups of forest trees. *Ecology* 70: 536–538.