Sambhu, Hemchandranauth, Northfield, Tobin, Nankishore, Alliea, Ansari, Abdullah, and Turton, Steve (2017) *Tropical rainforest and human-modified landscapes support unique butterfly communities that differ in abundance and diversity.* Environmental Entomology, 46 (6). pp. 1225-1234.

http://dx.doi.org/10.1093/ee/nvx129

Sambhu et al.: Butterfly abundance
and diversity in different land uses

Journal of Environmental Entomology
Community and Ecosystem Ecology

Hemchandranauth Sambhu
College of Science & Engineering
James Cook University, Cairns Campus
14-88 McGregor Road, Smithfield,
Queensland 4870, Australia
Mobile: (61) 040 679 0714
E-mail: hemchandranauth.sambhu@my.jcu.edu.au

Tropical rainforest and human-modified landscapes support unique butterfly communities that differ in abundance and diversity

Hemchandranauth Sambhu[1,2], Tobin Northfield[1], Alliea Nankishore, Abdullah Ansari[2], Stephen Turton[1,3]

[1] College of Science and Engineering, James Cook University, Cairns Campus, 14-88 McGregor Road, Smithfield, Queensland 4870, Australia.

[2] Department of Biology, Faculty of Natural Sciences, University of Guyana, Turkeyen, Greater Georgetown, Guyana.

[3] Central Queensland University, Cnr Shields and Abbott Streets, Cairns City, Queensland 4870, Australia.

Abstract

Tropical forests account for at least 50 percent of documented diversity, but anthropogenic activities are converting forests to agriculture and urban areas at an alarming rate, with potentially strong effects on insect abundance and diversity. However, the questions remain whether insect populations are uniformly affected by land conversion, and if insect conservation can occur in agricultural margins and urban gardens. We compare butterfly populations in tropical secondary forests to those found in sugarcane and urban areas in coastal Guyana and evaluate the potential for particular butterfly communities to inhabit human-modified landscapes.

Butterflies were sampled for one year using fruit-baited traps in three separated geographical locations on the coast. We used non-metric multidimensional scaling to assess differences in species assemblages and a generalized linear mixed model to evaluate abundance, species richness, evenness and diversity. The secondary forests in all three locations supported higher butterfly abundance and diversity than other human-modified areas, although the magnitude of this effect varied by season and location. However, each land use supported its own type of butterfly community, as species composition was different across the three land uses. Sugarcane field margins and urban gardens supported populations of butterflies rarely found in our tropical secondary forest sites. Land management practices that encourage forest conservation along with butterfly-friendly activities in human settlements and agricultural areas could improve butterfly conservation. To this end, butterfly conservation in Guyana and other tropical landscapes would benefit from a shift from inadvertently to actively making the landscape attractive for butterflies.

Key words: Guyana; land use; sugarcane plantation; tropical butterflies; urban.

Tropical countries have experienced extensive losses in forest cover in recent years (FAO 2016) and these have been largely attributed to corresponding increases in agricultural areas (Sodhi 2008, FAO 2016). In 2005, the Millennium Ecosystem Assessment (MEA) estimated that one quarter of the earth's terrestrial surface is covered by cultivation systems. Sugarcane (*Saccharum officinarum* L., 1753) cultivation generally results in declines in suitable food and habitat that support high biodiversity (Maes and Van Dyck 2001, Benton et al. 2003, Van Dyck et al. 2009). High nutrient inputs and the monoculture plantation style of sugarcane cultivation can also have significant negative impacts on soil health and its productive capabilities (Bell et al. 2007).

In addition to intensive agricultural practices, tropical countries experience the pressures of a growing human population, with an increase of 3.1 billion between 1950 and 2000 and a projected further increase of 2 billion before 2030 (UN 2004). Although the rate of natural forest loss has slowed, the tropics will likely continue to experience considerable declines in natural forest area (FAO 2016) as a result of the food, shelter and economic development needs of this growing human population, with perceived "luxuries" such as biodiversity conservation being overlooked (Sodhi 2008).

Given these changes, it is important to investigate how crop cultivation and expanding settlements are impacting landscapes as well as how these impacts are being managed (McLaughlin 2011). The future of tropical biodiversity and human well-being depend – more than ever – on the effective management of human-modified landscapes (Francesconi et al. 2013), with a balance between human activities (*e.g.*, intensive agriculture and expansion of settlements) and biodiversity conservation (Hodgson et al. 2010) as the desired outcome.

Biodiversity is frequently used as a proxy to evaluate the impacts of landscape changes on the health of the ecosystem (Meffe et al. 2006). Insects make up more than half of the documented global biodiversity (Fermon et al. 2000) and are commonly used to investigate disturbances in tropical forests (*e.g.*, King et al. 1998, Rodríguez et al. 1998, Jones and Eggleton 2000, Arellano et al. 2005).

Numerous studies have identified butterflies as effective indicators of habitat degradation (*e.g.*, Kremen 1992, Daily and Ehrlich 1995, Schulze et al. 2004, Bonebrake et al. 2010, Nyafwono et al. 2014). This is because they are sensitive to changes in habitat quality (Maes and Van Dyck 2001), are critical to the functioning of many ecosystems, and provide a wide range of ecosystem services including pollination of crops and selective herbivory of weeds (Summerville et al. 2004). Butterflies are also abundant, have a relatively quick generational turn over, and are easy to sample and identify (Brown 1997, Thomas 2005, Barlow et al. 2007).

Urbanization, road construction and intensive agriculture were reported to be responsible for at least 30 percent loss of butterfly species in Belgium (Maes and Van Dyck 2001), and the tropics are facing similar but accelerating anthropogenic pressures (Laurance et al. 2009). Although approximately 90 percent of all documented butterflies are found in the tropics, little is known about their ecology compared to temperate species (Bonebrake et al. 2010, Basset et al. 2011, Basset et al. 2012, DeVries et al. 2012). Insufficient knowledge can be a rate-limiting obstacle to biodiversity conservation, particularly in tropical countries (Wilson et al. 2016), suggesting a need for the development and implementation of appropriate and effective management strategies for butterfly biodiversity conservation in tropical landscapes (Chazdon et al. 2009).

As human-modified landscapes are a prominent and expanding feature in many tropical countries, they must be included in any conservation effort, and biological conservation in these landscapes can be useful for improving species abundances (Brockerhoff et al. 2008, Chazdon et al. 2009, Tabarelli 2010, da Rocha et al. 2012, Ellis 2013, Melo et al. 2013, Warren-Thomas et al. 2015). We evaluated butterfly community abundance, richness, evenness, diversity and composition across three land uses: tropical secondary forest, agriculture with a focus on sugarcane cultivation, and urban, in coastal Guyana. Given the benefits of conserving tropical secondary forests for maintaining biodiversity (Chazdon et al. 2009), we hypothesized that butterfly abundance, richness, evenness and diversity would be highest in tropical secondary forests, as has been found elsewhere in tropical primary forests (Barlow et al. 2007). We also hypothesized that agricultural areas and human settlements would support unique communities comprising butterfly species that have become adapted to the conditions created within these landscapes. Furthermore, we hypothesized that butterfly abundances in agricultural areas and human settlements would be less affected by within-seasonal patterns, due to consistency of external inputs such as irrigation, fertilizers, etc., than in tropical secondary forests that depend on seasonal rainfall patterns. This is in contrast to established theory, that because agricultural systems are classified as highly disturbed and low species diversity, they should be characterized by low temporal stability (Tscharntke et al. 2005). In sum, evaluating variation in community composition and dynamics across the different land use types could ultimately inform biodiversity conservation in tropical landscapes.

Materials and Methods

Study area

Our study was conducted in Guyana, South America, along sections of the coastal belt during the calendar year 2015. The coastal belt stretches from the Corentyne River (bordering with Suriname) in the east to Shell Beach (bordering with Venezuela) in the west and is approximately 459 km in length and 25 km in width inland from the Atlantic Ocean. It supports approximately 80 percent of the human population, with the estimated total population being 751,223 (GBS 2013). The vegetation types along the coastal belt include natural and secondary forests, agricultural crops – ranging from large-scale monocrop plantations of rice and sugarcane to small- or subsistence-scale crops, remnant and replanted mangrove forests, urban vegetation (lawns, flower patches, etc.), and abandoned or unmanaged farm lands that have reverted to forests.

The coastal climate is tropical and equatorial with four distinct seasons, two dry and two wet. The dry seasons occur from February to April (average rainfall: 84 mm per month) and August to October (average rainfall: 60 mm per month) (Guyana Hydrometerological Department, unpublished data). The wet seasons are from November to January (average rainfall: 150-300 mm per month) and May to July (average rainfall: 250-450 mm per month). The average air temperature is between 25- 27.5°C throughout the year (McSweeney et al. 2008).

Study sites were selected based on the following criteria:

(1) Accessibility to areas under the three selected land management practices: human settlement, agriculture and forest (secondary);
(2) Human population > 1000 persons per 10 km^2 in urban areas;
(3) Sugarcane monocrop plantations > 10 km^2 in agricultural areas; and
(4) Forested (secondary) area > 10 km^2.

The use of secondary (at least 25 years or older), rather than primary forested areas was due to a lack of enough suitable, accessible primary forest sites in the region. The secondary forest sites used in the study were similar in many regards. They were mixed forests that experienced similar levels of disturbance (few trees removed to construct shacks/houses, with small-scale short-term subsistence agriculture in open gaps). They were between 10 and 13 m high and with a canopy cover between 65-80% at each trap. The soil is fluvial with varying levels of clay.

Based on these criteria, the following three localities were selected along the coastline.

(1) La Bonne Intention (LBI)
(2) Tain
(3) Skeldon

Sampling of butterflies

To investigate butterfly abundance and diversity, three 1 km transects were randomly placed – separated by 1-1.5 km – in each of the land use zones (human settlement, agriculture and secondary forest) along existing access trails and roads (Supp. Fig. S1). Transects began at least 100 m from the hard edge of the land use zone in order to avoid possible edge effects. Transects in the secondary forests were laid out to utilize existing trails in an effort to minimize habitat disturbance (construction of new trails) as well as disruptions to butterfly behavior and other forest users. Because these transects followed the existing trails, they only followed straight lines when possible (Supp. Fig. S1). Those in agricultural areas were established along access roads within sugarcane plantations in an effort to reduce the impact of the research on the farmers’ crop and activities (*e.g.*, cultivation, harvesting). In urban areas, transects were set out along secondary roads or streets. The established transects were visited every month for 12 months (starting from January 2015 and ending in December 2015), so as to account for seasonality.

Butterflies were captured using baited cylindrical traps made of a 30 cm diameter white acrylic disk, white mosquito netting at a height of 90 cm and white string – based on the designs and techniques of DeVries (1987), Sambhu (2009) and Aduse-Poku et al. (2012). Traps were placed 100 m apart along each transect, starting at the 0 m marker and ending at the 1 km marker, for a total of 11 traps per transect (Supp. Fig. S1). Each trap was labeled with a unique number and geo-referenced to assist in the development of species distribution maps. The traps were placed approximately 1.5 m above ground to ensure easy access and baited with approximately 100 g of a fruit substance, fermented overnight and consisting of pureed over-ripe bananas (*Musa* sp. L., 1753), 4.7 percent alcohol per volume of 275 mL beer and brown cane sugar (4.5 kg of banana + 4 beers + 1 kg of sugar; as in Sambhu 2009 and Nyafwono et al. 2014). They were checked daily between 0800 h and 1600 h over a three-day period every month to reduce the bias of daily temperature fluctuation, which influences the exothermic (flight) nature of butterfly (Sands and New 2002). Traps were re-baited on an as-needed basis during the three-day checking period.

The trapping method was not intended to capture all butterfly species present, as the stratification and ecological niches of the various species makes this difficult to achieve. However, fruit-baited traps are one of the most reliable and unbiased methods for sampling tropical fruit-feeding butterflies (Daily and Ehrlich 1995, Hughes et al. 1998). By focusing on a low strata single feeding guild (fruit-feeding), this method allowed for comparisons (Francesconi et al. 2013) among the three contrasting land management practices under investigation. The issue of stratification within the three habitats (secondary forests with tree canopy, sugarcane plantations with no canopy and urban sites with varying presence/level of canopy) was reduced, as canopy butterfly species are often distinct from ground level species and were therefore unlikely to be collected in our traps (Dumbrell and Hill 2005, Aduse-Poku et al. 2012). However, some canopy-dwelling butterflies are not exclusive to canopies

(Aduse-Poku et al. 2012) and the presence of fruit bait at ground level can attract them, so this trapping method also does not completely exclude canopy-dwelling butterflies.

Each collected butterfly was placed in an individual envelope and information pertaining to the locality, transect number, trap number, date, name of collector, weather condition, unique identification number, sex and species (if known) were recorded on the envelope and in a field notebook at the trap site. Envelopes were stored in plastic containers and transported to the Center for the Study of Biological Diversity (CSBD) at the University of Guyana for identification.

Butterflies were identified with the aid of reference publications (D'Abrera 1984, DeVries 1987, Neild 1996, DeVries 1997, Darwin Initiative Butterfly Project Team - Guyana 2007, Neild 2008), the reference collection at the CSBD and the expertise of Drs. Blanca Huertas and Bernard Hermier. Butterflies were kept in cold storage (approximately 10°C) during the identification process to prevent decay or attack from predators. All of the collected butterflies were deposited at the CSBD (national repository) following identification.

Data analyses

We investigated differences in species composition using non-metric multidimensional scaling (NMDS) ordination, based on a Bray-Curtis dissimilarity matrix and Ward clustering. Winfree *et al*. (2011) discussed the importance of examining species composition in identifying possible generalist/specialist species tradeoffs in anthropogenic habitats. Before conducting NMDS ordination, the densities of each butterfly species were summed across the different traps and dates for a given land use, locality and season (comprising two wet and two dry seasons). The (x, y) coordinates of each land use, locality and season were then generated to identify species responsible for each cluster on the NMDS plot, and we evaluated differences in the resulting clusters through analysis of similarities (ANOSIM). These analyses were undertaken using the *Vegan* package (Oksanen et al. 2016) in *R*, *v 3.2.3* (R Core Team 2015).

The habitat specificity index (*Sm*) was calculated for butterfly species collected, where *Sm* is the number of individuals in the preferred habitat/ total number of individuals. Each species was placed in one of the following categories: (a) habitat specialist or species that had a single habitat supporting majority of its population: species with $Sm > 0.9$; (b) species with preference for a particular habitat but not necessarily a specialist of that habitat: species with $0.5 < Sm < 0.9$; and (c) habitat generalist or species that had no single habitat supporting majority of its population: species with $Sm < 0.5$. Only species populations with five or more individuals were used in this calculation as *Sm* is sensitive to sample size (Brito et al. 2014).

Rank abundance plots were also generated in *R*, *v. 3.2.3* for each land use type within each month as a display of relative species abundances or species abundance distributions. This was done so as to increase our understanding of the degree of biotic homogenization within the different land use types, which could impact on their conservation likelihood.

In addition to our multivariate analyses, we evaluated four univariate variables for each season, land use and locality: (1) abundance (total number of individuals in a particular subset); (2) species richness (S = total number of species in a particular subset); (3) diversity (Simpson's reciprocal index $(D) = 1/\Sigma(n/N)$^2, where n = total number of individuals of a particular species and N = total number of individuals in a particular subset); and (4) evenness (relative abundance of the different species in a particular subset: Simpson's index $(E) = (D/S)$. Migratory species, singletons and doubletons were included in our analyses as it is unclear if there were any unknown factors that were affecting the presence of some butterflies during this particular sampling period (DeVries and Walla 2001), or if the observed species numbers were as a result of any one of several reasons, including methodological limitations that inadvertently exclude individuals, genuinely small populations and/or low individual numbers across narrow scales (Novotný and Basset 2000). Plots were created and univariate values computed in *R*, *v. 3.2.3*; Simpson's diversity index was calculated using the *BiodiversityR* package (Kindt 2016).

A generalized linear mixed model (GLMM) with negative binomial distribution and a log-link function was used to analyze butterfly abundance and species richness across season and land use (fixed effects), with transect as a random effect. The negative binomial distribution accounts for the discrete, heteroscedastic nature of the count data. Locality was included in the model both as an independent factor (to test for an interaction with season) and as a nested factor of land use. This nested nature accounts for the possibility that each land use can vary among regions, and in particular, the nature of secondary forests may depend on the locality. A Toeplitz covariance structure was used to account for the temporal autocorrelation that was created by collecting butterflies from the same transects in different seasons. To improve parsimony, the months were grouped into greater seasons (wet, dry, wet, dry) for analyses. Species evenness and diversity were analyzed with the model structure as described above, but with a Gaussian distribution to account for the continuous rather than the discrete nature of the metrics. Differences were considered to be significant when $P < 0.05$. These analyses were undertaken using the *Glimmix* procedure in *SAS* ® software version 9.04 (SAS Institute Inc. 2015).

Results

Species composition

A total of 14,184 individuals belonging to 77 species within five families were captured over the 12-month study period. Sixty-three species (11,894 individuals) were captured in secondary forested areas, forty-three (1,403 individuals) from sugarcane plantations and thirty-three (887 individuals) from urban areas. Twenty-four species were common across the three land uses. Of the three localities sampled across all habitats, Tain and Skeldon both had sixty-four species (6,502 and 4,229 individuals, respectively) and LBI had fifty-three species (3,453 individuals). Forty-six species were common across all three localities. Additionally, higher numbers of individuals and species were caught in the dry seasons (8,530 individuals within seventy species) than in the wet seasons (5,654 individuals within sixty-five species), with forty-seven species common in both the wet and dry seasons (Supp. Table S1). The Bray-Curtis dissimilarity matrix for NMDS ordination revealed three distinct groups that signified variations in species composition (ANOSIM; R = 0.8085, $P = 0.0010$, Fig. 1). As expected, each group aligned with a defined land use and species fit neatly into these groups across localities and seasons, with one exception – sugarcane plantation species in LBI in the second wet season were more similar to urban areas in species composition.

Species richness and abundance

Average butterfly abundance was generally higher in the secondary forest across all localities than in the sugarcane plantation (8.5 times more collected across the year) and urban area (13.4 times more collected across the year) [Table 1 (land use main effect); Fig. 2A–C], but variations were evident throughout the year in all land uses. For example, a decrease in average abundance was observed at the beginning of the second dry season (August) in the secondary forest at Skeldon and LBI, with a simultaneous increase in abundance in the sugarcane plantations and urban areas of Skeldon. Additionally, butterfly abundance and richness declined during the second wet season (December) in Skeldon and Tain secondary forests. These variations in patterns of abundance throughout the year and across the different land uses led to a significant interaction among land use and season and locality and season – indicating that the differences in butterfly abundance across the three land use types and between localities varied seasonally (Table 1). In general, however, butterfly abundances differed by land use , locality and season.

Results show higher butterfly species richness in the secondary forest than in sugarcane plantations and urban areas (, but the magnitude of this difference depended on season Table 1; Fig. 2D–F). Similarly, species numbers varied significantly across localities, but this effect depended on season (Table 1).

The rank abundance plots (Fig. 3) show that the urban areas were mostly dominated by a single species compared to the other land uses, except in August when sugarcane plantations were dominated by *Historis acheronta* (F, 1775). A consistent pattern of species dominance was observed in the urban areas throughout the year, with *Opsiphanes cassina* (Felder and Felder, 1862) being the most dominant species in this land use – except in October when *Glutophrissa drusilla* (Cramer, 1777) was dominant. In sugarcane plantations, *Mnasilus allubita* (Butler, 1877) was dominant for the first four months of collection (January to April), after which other species were present in higher numbers for shorter periods of time. The secondary forest was dominated by *Morpho helenor* (Cramer, 1776) for eight months of the study period.

Patterns of evenness and diversity

When evaluated over a three-month season, sugarcane plantations had the highest overall evenness compared with the secondary forests and urban areas (Table 1; Fig. 4A–C). Evenness did not vary significantly across seasons (nor localities), but the magnitude of differences among the three land uses was considerable enough to result in a significant interaction between land use and season.

Like abundance and species richness, the secondary forests had the highest overall diversity than the other land uses (Table 1; Fig. 4D–F). Similar to the results obtained for evenness and despite apparent variations across seasons, however, the land use effect did not depend on season (nor locality) and drove the interaction between land use and season.

Discussion

Intensified agroecosystems (Harvey et al. 2006, Chazdon et al. 2009, Wilcove and Koh 2010) and human settlements (Koh and Sodhi 2004) often support few species compared to forest habitats, and are often dominated by the few species adapted to conditions specific to those systems (Root 1973, Alberti 2005, McKinney 2006). In our study, secondary forests supported a different assemblage of species from the sugarcane plantations and urban areas (Fig. 1). Forest species, and in particular the understory species our sampling focused on, rely on the presence of a closed canopy for feeding and ovipositing (Koh and Sodhi 2004). This closed canopy environment is generally absent from agricultural or urban landscapes, which may have influenced butterfly habitat suitability. Furthermore, these results (Figs. 2 and 4) support findings from a range of studies suggesting that land use intensification reduces species abundance and diversity (Tscharntke et al. 2005, Melo et al. 2013, Gossner et al. 2016). However, our results suggest that improving host availability in the more intensified landscapes (agriculture and urban areas) may help conserve species adapted for those environments. For example, the deliberate planting of coconut (*Cocos nucifera* L., 1753) plants in urban areas contributed to the change in butterfly species (*O. cassina*) composition of the area. Furthermore, maintaining uncultivated plants in field margins may support an array of butterfly species that are able to inhabit sugarcane agroecosystems. For example, the common occurrence of *Desmodium incanum* (DC, 1825) likely increases the abundance of *Urbanus dorantes* Stoll, 1790 (Cock 2015; see below for other examples).

Urban areas comprise of a mixture of open and closed canopies (Koh and Sodhi 2004), due to variation in personal preference for gardening and landscaping vegetation types. Additionally, the intensity of synthetic chemical (*e.g.*, pesticides, fertilisers) usage tends to be lower in these areas when compared to agricultural areas (Brown Jr. and Freitas 2002). The differences in conditions between sugarcane plantation and urban area settings therefore may drive differences in butterfly species composition between the two land uses.

Sugarcane plantations supported over 50 percent of the collected species, of which 14 species (18 percent of the species collected) (*Agraulis vanillae* L., 1758; *Aphrissa statira* Cramer, 1777; *Atalopedes campestris* Boisduval, 1852; *Calpodes ethlius* Stoll, 1782; *Dryadula phaetusa* L., 1758; *Euptoieta hegesia* Cramer, 1779; *Hemiargus ceraunus* F., 1793; *Historis acheronta*; *Mnasilus allubita*; *Phoebis argante* F., 1775; *P. sennae* L., 1758; *Urbanus dorantes*; *Urbanus procne* Plötz, 1881; and *Vehilius celeus* Mabille, 1891) showed a strong habitat preference for this land use. Species such as *U. procne*, *E. hegesia* and *A. campestris* had ample presence of suitable host plants [*Cynodon dactylon* (L., 1753; Kendall 1966), *Turner ulmifolia* (L., 1753; Schappert and Shore 1998) and weed grasses (Crozier 2004), respectively] for larval development. Others [*P. sennae* (Srygley 2001), *P. argante, A. statira* and *H. acheronta* (Srygley and Dudley 2008)] were known migratory species with resident populations that made use of resources within the study locations, which were also part of the migration path of *H. acheronta* as suggested by its high numbers during the first wet season and the second dry season (17.4 percent and 77.2 percent, respectively, of total *H. acheronta* collected in sugarcane areas; Supp. Table S1; Fig. 3). Sugarcane plantations generally had more even butterfly communities (Fig. 4A–C) compared to secondary forests and urban areas. This occurred because sugarcane plantations had fewer species than the other land use types that occurred in low relative abundance. Tropical forests often support diverse insect communities that include a number of rare species feeding on similarly rare plants species (Novotný and Basset 2000), and the conservation of rare species can sometimes be associated with either no change in evenness or even reduced evenness compared to communities with lower species richness (Smith and Wilson 1996, Crowder et al. 2012).

The secondary forest contained 30 specialists within the following subfamilies: Biblidinae (3), Charaxinae (4), Morphinae (10), Nymphalinae (2) and Satyrinae (10), with *Morpho helenor* being the dominant species for eight of the 12 surveyed months. It was interesting to note that none of the strong flyers, such as *Morpho* and *Archaeoprepona* (Fruhstorfer, 1915) species, ventured into the other land use types, as Brito et al. (2014) suggested that strong flyers would explore different habitats that experienced different levels of disturbance. The dominance of *M. helenor* in secondary forests can be attributed to the ability of this species to exploit microhabitat conditions (*e.g.*, sunlight patches with contrasting shade for basking and display) and nutritional resources (*e.g.*, *Inga* sp. trees as larval host) within different seasons.

Urban areas supported lower species richness than the other land use types (39 percent and 14.3 percent lower than forested and urban areas, respectively), with only three species (*Anartia jatrophae* L., 1763; *Glutophrissa drusilla*, *Opsiphanes cassina*) having higher individual counts than in secondary forests (88.64, 44.35 and 61.43 lower percentages, respectively; Supp. Table S1) and sugarcane plantations (90.91, 22.61 and 73.91 lower percentages, respectively; Supp. Table S1). *A. jatrophae*, classed as an urban specialist, occurred mostly during the first wet and second dry season, with the adult obtaining nectar from plants such as *Bidens pilosa* (L., 1753) and *Lantana camara* (L., 1753; Fernández-Hernández 2007) and the larvae feeding on species of *Ruellia* (L., 1753) and *Lippia* (L., 1753; Knerl and Bowers 2013), all of which are common weeds within the urban landscape. *G. drusilla* was seen to be dominant only in October when one of its nectar plants (*Antigonon leptopus* Hook and Arn, 1838) was in full bloom. Alternatively, *O. cassina* was dominant throughout most of the year in urban areas (Fig. 3) having the constant presence of available larval host plants (palm trees) (Vasquez et al. 2008) to support it. Coconut palms are prevalent throughout coastal Guyana as an important multiple use crop (*e.g.*, food, oil, animal stockfeed, household cleaning agent, cultural decorations) to many homesteads, so these are used as the larval host plant by *O. cassina*. It is interesting to note that *O. cassiae* (L., 1758) was classified as a forest specialist, while *O. cassina* showed a strong preference for the urban habitat. The habitat association by these two similar species, along with that of *Taygetis echo* (Cramer, 1775; a forest specialist) and *T. laches* (F., 1793; not a specialist, but showed a preference for the forest), does not support the proposition that subfamily composition comparison is adequate in understanding species natural history (Francesconi et al. 2013).

We found lower variation in butterfly abundance and richness in the human-modified areas compared to secondary forests, potentially due to the consistency of external inputs such as irrigation and fertilization in such landscapes. In contrast, natural areas exhibit larger fluctuations in water availability, with increased production of plant foliage biomass during wet seasons promoting growth and survival of larval stages (Aide 1992). However, this simplistic pattern is not always adhered to because of unpredictable weather variations that alter the timing and manner in which plants modify their foliage, so spillovers can occur where there are delays in ovipositing and/or adults eclosing (Nobre et al. 2012). Where the decreases in butterfly abundance were evident in our study (*e.g.*, at the beginning of the second dry season/August in Skeldon and LBI secondary forests), it is likely that conditions were not suitable for the adult forms so catch numbers were low. It is unclear why this decrease did not occur in the Tain region. Declines that also occurred during the second wet season (December) in Skeldon and Tain forests for both abundance and species richness can be attributed to the fruiting of forest plant species (such as *Attalea butyracea* L., 1781) and therefore the availability of alternative food resources for fruit-feeding butterflies. This may have reduced fruit-baited trap attractiveness during this period (Barlow et al. 2007), potentially lowering our traps focused on the fruit-feeding butterflies. Some trap bias is a common occurrence in trap-based studies (*e.g.*, Biro and Stamps 2008).

Other factors can interact with seasonality in human-modified areas to alter butterfly abundance and richness. For example, in Guyana, sugarcane is harvested during the dry season by sectional burning and slashing, which can cause damage to host plants. As sugarcane is harvested only during the dry seasons, these landscape changes add to the seasonality effect on butterflies. Similarly, in urban areas in Guyana, most households do landscaping (including gardening) primarily during the dry seasons when conditions are favorable for such outdoor activities. This seasonal effect of human disturbance during the dry season in these two human-modified areas adds to the seasonality effect on butterflies in such areas, thus reducing support for our second hypothesis that butterfly abundance would be less affected by seasonality in human-modified areas.

Although butterfly abundance and species richness were lower in human-modified landscapes, some human activities may help to support viable populations and habitat specialists that are not found in forested landscapes. In our study areas, these activities included people inadvertently fostering a healthy butterfly community in their quest to beautify their environs (*e.g.*, planting of *Ixora* spp. which flowers throughout the year, thus providing a food source all year) and also through the maintenance of permanent irrigation systems and inefficient weed management practices within agricultural lands as well as residential areas. Irrigation of sugarcane in Guyana is not done actively via a mechanized system but instead through irrigation canals (along the eastern side of the cultivation plot) within which high water levels are permanently maintained and drainage canals (on the western side of the plots). Additionally, while weeds within cultivation plots are stringently managed, those along access roads to the plots are not controlled/eradicated as to do so would be costly to the industry, and these uncultivated areas may benefit butterflies (Miller et al. 2011). Butterfly diversity can be further enhanced by the planting of shelter, host and nectar plants along the banks of drainage canals (along the access roads), so as to act as a corridor of host plants and/or post-harvest windbreaks within which butterflies can traverse or possibly become established. These corridors, which will not impede on any of the sugarcane cultivation and harvesting operations, could possibly allow some of the forested species, especially the strong fliers, to explore more habitats (Haddad and Tewksbury 2005, Tscharntke et al. 2005).

While human-modified areas can be seen as having largely negative impacts on biodiversity and conservation efforts on several species, they still provide critical space and resources for other species. This supports our hypothesis that human-modified landscapes can support viable populations of certain species, and has important implications for the inclusion of these landscapes in the design and implementation of area-specific biodiversity management policies in the tropics. It is increasingly difficult to maintain pristine forest conditions in the tropics (Bruner et al. 2004, Melo et al. 2013), both from an economic standpoint and with the pressures of human population growth. While, for good reason, we stress the need for the continuous protection of old-growth/natural forests, it would also be sensible to deliberately enhance human-modified landscapes so as to encourage more butterfly-friendly spaces as well as to improve the likelihood of long-term persistence of butterfly species and biodiversity in general.

Conclusion

Butterfly abundance, richness and diversity were higher in secondary forests in coastal Guyana than in nearby agricultural and urban areas. However, species composition of the three land uses was significantly different, with human-modified areas (*i.e.*, sugarcane plantations and urban areas) comprising species (both habitat specialists and those with preference for the respective human-modified areas) that have adapted to more open canopy conditions and have modified their host and nectar plant preferences. As each land use is supportive of its own type of butterfly community, human-modified areas do not universally represent a threat to biological diversity. Thus, biodiversity conservation planners and land managers should facilitate the conservation of forested areas and simultaneously encourage more gardening in homesteads in human settlements as well as conservation of field margins within agricultural areas. Given that the human settlements in Guyana and across the tropics will continue to expand with housing developments and accompanying agricultural production systems, it is essential for land managers and conservationists to consider the human-modified areas as a source/sink area for biodiversity (butterflies, in particular). Improving conservation efforts in these areas modified by human behavior may be an important component for maintaining populations of the butterfly species that inhabit these areas.

Acknowledgements

We are grateful to Blanca Hertas and Bernard Hermier for assisting with identification of specimens, Lalita Lallbeharry for helping with storage of the collected butterflies during the survey period, Savitri Mohan for providing bananas to make the butterfly bait, Devendra Peritomby for providing accommodation during data collection at the Tain site, David Cassells and Amy Diedrich for their encouragement, and the residents who supported the survey by allowing for traps to be set up on their property. Our study would not have been possible without the kind support of the Guyana Sugar Corporation, especially the staff of the Skeldon, Tain and LBI estates, who provided assistance in the planning and execution of logistics as well as field assistants to conduct the survey. Also, we thank the University of Guyana and the CSBD for access to reference collections, the Guyana Environmental Protection Agency for issuing the necessary permits, the Guyana Hydrometeorological Department for providing meteorological data for the different sites, and finally the Guyana Wildlife Division for funding support.

References

Aduse-Poku, K., O. William, S. K. Oppong, T. Larsen, C. Ofori-Boateng, and F. Molleman. 2012. Spatial and temporal variation in butterfly biodiversity in a West African forest: lessons for establishing efficient rapid monitoring programmes. *Afr. J. Ecol.* 50: 326–334.

Aide, T. M. 1992. Dry season leaf production: an escape from herbivory. *Biotropica* 24: 532–537.

Alberti, M. 2005. The effects of urban patterns on ecosystem function. *Int. Reg. Sci. Rev*. 28: 168–192.

Arellano, L., M. E. Favila, and C. Huerta. 2005. Diversity of dung and carrion beetles in a disturbed Mexican tropical montane cloud forest and on shade coffee plantations. *Biodivers. Conserv*. 14: 601–615.

Barlow, J., W. L. Overal, I. S. Araujo, T. A. Gardner, and C. A. Peres. 2007. The value of primary, secondary and plantation forests for fruit-feeding butterflies in the Brazilian Amazon. *J. Appl. Ecol*. 44: 1001–1012.

Basset, Y., R. Eastwood, L. Sam, D. J. Lohman, V. Novotny, T. Treuer, S. E. Miller, G. D. Weiblen, N. E. Pierce, S. Bunyavejchewin, W. Sakchoowong, P. Kongnoo, M. A. Osorio-Arenas. 2011. Comparison of rainforest butterfly assemblages across three biogeographical regions using standardized protocols. *J. Res. Lepid*. 44: 17–28.

Basset, Y., R. Eastwood, L. Sam, D. J. Lohman, V. Novotny, T. Treuer, S. E. Miller, G. D. Weiblen, N. E. Pierce, S. Bunyavejchewin, W. Sakchoowong, P. Kongnoo, and M. A. Osorio-Arenas. 2012. Cross-continental comparisons of butterfly assemblages in tropical rainforests: implications for biological monitoring. *Insect Conserv. Divers*. 6: 223–233.

Bell, M. J., G. R. Stirling, and C. E. Pankhurst. 2007. Management impacts on health of soils supporting Australian grain and sugarcane industries. *Soil Tillage Res*. 97: 256–271.

Benton, T. G., J. A. Vickery, and J. D. Wilson. 2003 Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 18: 182–188.

Biro, P. A., and J. A. Stamps. 2008. Are animal personality traits linked to life-history productivity? *Trends Ecol. Evol.* 23: 361–368.

Bonebrake, T. C., L. C. Ponisio, C. L. Boggs, and P. R. Ehrlich. 2010. More than just indicators: a review of tropical butterfly ecology and conservation. *Biol. Cons*. 143: 1831–1841.

Brito, M. M., D. B. Ribeiro, M. Raniero, E. Hasui, F. N. Ramos, and A. Arab. 2014. Functional composition and phenology of fruit-feeding butterflies in a fragmented landscape: variation of seasonality between habitat specialist. *J. Insect Conserv*. 18: 547–560.

Brockerhoff, E. G., H. Jactel, J. A. Parrotta, C. P. Quine, and J. Sayer. 2008. Plantation forests and biodiversity: oxymoron or opportunity? *Biodivers. Conserv*. 17: 925–951.

Brown, K. S. 1997. Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. *J. Insect Conserv*. 1: 25–42.

Brown Jr., K. S., and A. V. L. Freitas. 2002. Butterfly communities of urban forest fragments in Campinas, São Paulo, Brazil: structure, instability, environmental correlates, and conservation. *J. Insect Conserv*. 6: 217–231.

Bruner, A. G., R. E. Gullison, and A. Balmford. 2004. Financial costs and shortfalls of managing and expanding protected-area systems in developing countries. *BioScience*. 54: 1119–1126.

Chazdon, R. L., C. A. Harvey, O. Komar, D. M. Griffith, B. G. Ferguson, M. Martínez-Ramos, H. Morales, R. Nigh, L. Soto-Pinto, M. van Breugel, and S. M. Philpott. 2009. Beyond reserves: a research agenda for conserving biodiversity in human-modified tropical landscapes. *Biotropica*. 41: 142–153.

Cock, M. J. W. 2015. Observations on the biology of skipper butterflies in Trinidad, West Indies: *Urbanus, Astraptes* and *Narcosius* (Hesperiidae: Eudaminae). *Living World, J. Trinidad and Tobago Field Naturalists' Club*. ISSN 1029-3299: 1–14.

Crowder, D. W., T. D. Northfield, R. Gomulkiewicz, and W. E. Snyder. 2012. Conserving and promoting evenness: organic farming and fire-based wildland management as case studies. *Ecology*. 93: 2001–2007.

Crozier, L. G. 2004. Field transplants reveal summer constraints on a butterfly range expansion. *Oecologia*. 141: 148–157.

D'Abrera, B. 1984. Butterflies of South America. Hill House, Australia.

da Rocha, P. L. B., B. F. Viana, M. Z. Cardoso, A. M. C. de Melo, M. G. C. Costa, R. N. de Vasconcelos, and T. B. Dantas. 2012. What is the value of eucalyptus monocultures for the biodiversity of the Atlantic forest? A multitaxa study in southern Bahia, Brazil. *J. For. Res*. 24: 263–272.

Daily, G. C., and P. R. Ehrlich. 1995. Preservation of biodiversity in small rainforest patches - rapid evaluations using butterfly trapping. *Biodivers. Conserv*. 4: 35–55.

Darwin Initiative Butterfly Project Team - Guyana. 2007. An introduction to butterflies of the Iwokrama forest and communities of the North Rupununi District, Guyana, South America. Darwin Initiative, London, United Kingdom.

DeVries, P. J. 1987. The butterflies of Costa Rica and their natural history: Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Baskerville, USA.

DeVries, P. J. 1997. The butterflies of Costa Rica and their natural history: Riodinidae. Princeton University Press, United Kingdom.

DeVries, P. J., and T. R. Walla. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. *Biol. J. Linnean Soc*. 74: 1–15.

DeVries, P. J., L. G. Alexander, I. A. Chacon, J. A. Fordyce. 2012. Similarity and difference among rainforest fruit-feeding butterfly communities in Central and South America. *J. Anim. Ecol*. 81: 472–482.

Dumbrell, A. J., and J. K. Hill. 2005. Impacts of selective logging on canopy and ground assemblages of tropical forest butterflies: implications for sampling. *Biol. Cons*. 125: 123–131.

Ellis, E. C. 2013. Sustaining biodiversity and people in the world's anthropogenic biomes. *Curr. Opin. Environ. Sustain*. 5: 368–372.

EPA-Guyana. 2007. National biodiversity action plan II: a continued programme for action by stakeholders towards conservation and sustainable use of biodiversity. Environmental Protection Agency, Guyana. < https://www.google.com.au/url?sa=t&rct=j&q=&esrc=s&source=web&cd=1&cad=rja&uact=8&ved=0ahUKEwj7q6bw4MfOAhVCpZQKHc51Ag8QFggbMAA&url=https%3A%2F%2Fwww.cbd.int%2Fdoc%2Fworld%2Fgy%2Fgy-nbsap-v2-en.pdf&usg=AFQjCNFOYjFYK14hCx-1yKHU1QCJcjwxjg&bvm=bv.129759880,d.dGo> 17th August, 2016.

FAO. 2016. Global forest resources assessment 2015: how are the world's forests changing? Second edition. Food and Agriculture Organization of the United Nations, Rome. <http://www.fao.org/forest-resources-assessment/en/> 16th September, 2016.

Fermon, H., M. Waltert, T. B. Larsen, U. Dall'Asta, and M. Mühlenberg. 2000. Effects of forest management on diversity and abundance of fruit-feeding Nymphalid butterflies in South-eastern Côte d'Ivoire. *J. Insect Conserv*. 4: 173–189.

Fernández-Hernández, D. M. 2007. Butterflies of the agricultural experiment station of tropical roots and tubers, and Santa Ana, Camagüey, Cuba: an annotated list. *Acta Zool. Mex*. 23: 43–75.

Francesconi, W., P. K. R. Nair, D. J. Levey, J. Daniels, and L. Cullen Jr. 2013. Butterfly distribution in fragmented landscapes containing agroforestry practices in Southeastern Brazil. *Agrofor*. *Syst*. 87: 1321–1338.

GBS. 2013. Census report (2002). Guyana Bureau of Statistics, Government of Guyana. < http://www.statisticsguyana.gov.gy/census.html#popcenfinal> 17th August, 2016.

Gossner, M. M., T. M. Lewinsohn, T. Kahl, F. Grassein, S. Boch, D. Prati, K. Birkhofer, S. C. Renner, J. Sikorski, T. Wubet, H. Arndt, V. Baumgartner, S. Blaser, N. Blüthgen, C. Börschig, F. Buscot, T. Diekötter, L. Re'Jorge, K. Jung, A. C. Keyel, A. Klein, S. Klemmer, J. Krauss, M. Lange, J. Müller, J. Overmann, E. Pašalić, C. Penone, D. J. Perović, O. Purschke, P. Schall, S. A. Socher, I. Sonnemann, M. Tschapka, T.Tscharntke, M. Türke, P. C. Venter, C. N. Weiner, M. Werner, V. Wolters, S. Wurst, C. Westphal, M. Fischer, W. W. Weisser, and E. Allan. 2016. Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* 540: 266–269.

Haddad, N. M., and J. J. Tewksbury. 2005. Low-quality habitat corridors as movement conduits for two butterfly species. *Ecol. Appl.* 15: 250–257.

Hall, J. P. 2006. A remarkable new riodinid species, *Stalachtis halloweeni* (Riodinidae: Stalachtini), from Mount Ayanganna, Guyana. *J. Lepid. Soc*. 60: 138–142.

Harvey, C. A., J. Gonzalez, and E. Somarriba. 2006. Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. *Biodivers. Conserv*. 15: 555–585.

Hodgson, J. A., W. E. Kunin, C. D. Thomas, T. G. Benton, and D. Gabriel. 2010. Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. *Ecol. Lett*. 13: 1358–1367.

Hughes, J. B., G.C. Daily, and P. R. Ehrlich. 1998. Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). *Rev. Biol. Trop*. 46: 697–704.

Jones, D. T., and P. Eggleton. 2000. Sampling termite assemblages in tropical forests: testing a rapid biodiversity assessment protocol. *J. Appl. Ecol*. 37: 191–203.

Kendall, O. 1966. Larval food plants for five Texas Hesperiidae. *J. Lepid. Soc*. 20: 35–41.

Kindt, R. 2016. BiodiversityR: package for community ecology and suitability analysis. Version 2.7-1. < https://cran.r-project.org/web/packages/BiodiversityR/index.html > 17th August, 2016.

King, J. R., A. N. Anderson, A. D. Cutter. 1998. Ants as bioindicators of habitat disturbance: validation of the functional group model for Australia's humid tropics. *Biodivers. Conserv*. 7: 1627–1638.

Knerl, A., and D. Bowers. 2013. Incorporation of an introduced weed into the diet of a native butterfly: consequences for preference, performance and chemical defense. *J. Chem. Ecol*. 39: 1313–1321.

Koh, L. P., and N. S. Sodhi. 2004. Importance of reserves, fragments and parks for butterfly conservation in a tropical urban landscape. *Ecol. Appl*. 14: 1695–1708.

Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecol. Appl*. 2: 203–217.

Laurance, W. F., M. Goosem, and S. G. W. Laurance. 2009. Impacts of roads and linear clearings on tropical forests. *Trends Ecol. Evol*. 24: 659–669.

McKinney M. L. 2006. Urbanization as a major cause of biotic homogenization. *Biol. Cons*. 127: 247–260.

McLaughlin, D. W. 2011. Land, food, and biodiversity. *Conserv. Biol*. 25: 1117–1120.

McSweeney, C., M. New, and G. Lizcano. 2008. UNDP climate change country profiles: Guyana. < http://ncsp.undp.org/country/guyana> 17th August, 2016.

Maes, D., and H. Van Dyck. 2001. Butterfly diversity loss in Flanders (north Belgium): Europe's worst case scenario? *Biol. Cons*. 99: 263–276.

Meffe, G. K., C. R. Carroll, and M. J. Groom. 2006. Principles of conservation biology. Sinauer Associates, Inc., Sunderland, Massachusetts.

Melo, F. P. L., V. Arroyo-Rodríguez, L. Fahrig, M. Martínez-Ramos, and M. Tabarelli. 2013. On the hope for biodiversity-friendly tropical landscapes. *Trends Ecol. Evol*. 28: 462–468.

Millennium Ecosystem Assessment. 2005. Ecosystems and human well-being: synthesis. Millennium Ecosystem Assessment, Island Press, Washington, D.C. < https://www.google.com.au/url?sa=t&rct=j&q=&esrc=s&source=web&cd=1&cad=rja&uact=8&ved=0ahUKEwiYrPOq5cfOAhXCkpQKHSKzDXkQFgggMAA&url=http%3A%2F%2Fwww.millenniumassessment.org%2Fdocuments%2Fdocument.356.aspx.pdf&usg=AFQjCNFz3RteV0yfEAgFKZzFaxa93xztGg&bvm=bv.129759880,d.dGo> 17th August, 2016.

Miller, D. G., J. Lane, and R. Senock, R. 2011. Butterflies as potential bioindicators of primary rainforest and oil palm plantation habitats on New Britain, Papua New Guinea. *Pac. Conserv. Biol*. 17: 149–159.

Nakahara, S., S. A. Fratello, and D. J. Harvey. 2014. A new species of *Euptychia* Hübner, 1818 (Lepidoptera: Nymphalidae: Satyrinae: Satyrini) from Mount Roraima, Guyana. *Zootaxa*. 3881: 291–300.

Neild, A. F. E. 1996. The butterflies of Venezuela: Nymphalidae I (Limenitidinae, Apaturinae, Charaxinae). Meridian Publications, Greenwich, London.

Neild, A. F. E. 2008. The butterflies of Venezuela. Part 2: Nymphalidae II (Acraeinae, Libytheinae, Nymphalinae, Ithomiinae, Morphinae). Meridian Publications, Greenwich, London.

Nobre, C. E. B., L. Iannuzi, and C. Schlindwein. 2012. Seasonality of fruit-feeding butterflies (Lepidoperta, Nymphalidae) in a Brazilian semiarid area. *ISRN Zoology*. 2012: 1–8.

Novotný, V., and Y. Basset. 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *OIKOS*. 89: 564–572.

Nyafwono, M., A. Valtonen, P. Nyeko, and H. Roininen. 2014. Butterfly community composition across a successional gradient in a human-disturbed Afro-tropical rainforest. *Biotropica*. 46: 210–218.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2016. Vegan: community ecology package. R package version 2.3-3. < https://CRAN.R-project.org/package=vegan> 17th August, 2016.

Pyrcz, T. W., and S. Fratello. 2005. Cloud forest butterfly fauna of the pantepui - poor or poorly known? Descriptions of new species and records of new genera of Pronophilina:

Eretris agata and *Oxeoschistus romeo* (Nymphalidae: Satyrinae). *J. Lepid. Soc*. 59: 200–211.

R Core Team. 2015. R: a language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/> 17th August, 2016.

Rodríguez, J. P., D. L. Pearson, and R. R. Barrera. 1998. A test for the adequacy of bioindicator taxa: are tiger beetles (Coleoptera: Cicindelidae) appropriate indicators for monitoring the degradation of tropical forests in Venezuela? *Biol. Cons*. 83: 69–76.

Root, R. B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol. Monograph*. 43: 95–124.

Sambhu, H. 2009. The feasibility of establishing a butterfly farm in Fairview village, North Rupununi, Guyana, South America. MSc. Thesis, University of Warwick, London.

Sands, D. P. A., and T. R. New. 2002. The action plan for Australian butterflies. Environment Australia, Canberra, Australia.

SAS Institute Inc. 2015. SAS version 9.04. Cary, NC, USA.

Schappert, P. J., and J. S. Shore. 1998. Ecology, population biology and mortality of *Euptoieta hegesia* Cramer (Nymphalidae) on Jamaica. *J. Lepid. Soc*. 52: 9–39.

Schulze, C. H., M. Waltert, P. J. A. Kessler, R. Pitopang, Shahabuddin, D. Veddeler, M. Mühlenberg, S. R. Gradstein, C. Leuschner, I. Steffan-Dewenter, and T. Tscharntke. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecol. Appl*. 14: 1321–1333.

Smith, B., and J. T. Wilson. 1996. A consumer's guide to evenness indices. *Oikos*. 76: 70–82

Sodhi, N. S. 2008. Tropical biodiversity loss and people - a brief review. *Basic Appl. Ecol*. 9: 93–99.

Srygley, R. B. 2001. Sexual differences in tailwind drift compensation in *Phoebis sennae* butterflies (Lepidoptera: Pieridae) migrating over seas. *Behav. Ecol*. 12: 607–611.

Srygley, R. B., and R. Dudley. 2008. Optimal strategies for insects migrating in the flight boundary layer: mechanisms and consequences. *Integr. Comp. Biol*. 48: 119–133.

Summerville, K. S., L. M. Ritter, and T. O. Crist. 2004. Forest moth taxa as indicators of lepidopteran richness and habitat disturbance: a preliminary assessment. *Biol. Cons*. 116: 9–18.

Tabarelli, M. 2010. Tropical biodiversity in human-modified landscapes: what is our trump card? *Biotropica*. 42: 553–554.

Thomas, J. A. 2005. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philos. Trans. R. Soc. London [Biol.]* 360: 339–357.

Tscharntke, T. A., M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity- ecosystem service management. *Ecol. Lett.*8: 857–874.

UN. 2004. World population to 2300. United Nations Department of Economic Social Affairs Population Division, New York.

Van Dyck, H., A. J. Van Strien, D. Maes, and C. A. M. Van Swaay. 2009. Declines in common, widespread butterflies in a landscape under intense human use. *Conserv. Biol.* 23: 957–965.

Vasquez, J., C. Delgado, G. Couturier, K. Mejia, L. Freitas, and D. Del Castillo. 2008. Pest insects of the palm tree *Mauritia flexuosa* L. f., dwarf form, in Peruvian Amazonia. *Fruits*. 63: 227–238.

Warren-Thomas, E., P. M. Dolman, and D. P. Edwards. 2015. Increasing demand for natural rubber necessitates a robust sustainability initiative to mitigate impacts on tropical biodiversity. *Conserv. Lett*. 8: 230–241.

Wilcove, D. S., and L. P. Koh. 2010. Addressing the threats to biodiversity from oil-palm agriculture. *Biodivers. Conserv*. 19: 999–1007.

Wilson, K. A., N. A. Auerbach, K. Sam, A. G. Magini, A. S. L. Moss, S. D. Langhans, S. Budiharta, D. Terzano, and E. Meijaard. 2016. Conservation research is not happening where it is most needed. *PLOS Biology*. 14: e1002413.

Winfree, R., I. Bartoumeus, and D. P. Cariveau. 2011. Native pollinators in anthropogenic habitats. *Annu. Rev. Ecol. Evol. Syst*. 42: 1–22.

Table Legends

Table 1. Results of the generalized linear mixed model analyses for each of the four response variables in our monthly surveys across three different localities (locality effect) over four seasons (2 wet seasons and 2 dry seasons; season effect), and three land uses (secondary forest, sugarcane plantation, human settlement; land use effect). We also used locality as a nested factor of land use and transect as a random effect. Additionally, a Toeplitz covariance structure was used to account for the temporal autocorrelation that was created by collecting butterflies from the same transects in different seasons.

Type III Tests of Fixed Effects			Abundance		Richness		Evenness		Diversity	
Effect	Num DF	Den DF	F	Pr > F	F	Pr > F	F	Pr > F	F	Pr > F
Locality	2	18	4.43	0.0272	9.46	0.0016	2.74	0.0912	0.78	0.4738
Land use	6	18	58.70	< 0.0001	61.54	< 0.0001	18.54	< 0.0001	32.83	< 0.0001
Season	3	53	23.61	< 0.0001	19.78	< 0.0001	1.07	0.3707	2.70	0.0548
Locality × season	6	53	11.66	< 0.0001	6.96	< 0.0001	2.12	0.0663	1.84	0.1092
Land use × season	18	53	6.19	< 0.0001	3.76	<0.0001	2.21	0.0134	3.35	0.0003

Figure Legends

Fig. 1. NMDS with Bray distance matrix and Ward's clustering of land uses, localities (Sk = Skeldon, Ta = Tain, Lb = LBI) and seasons (D1 = first dry season, W1 = first wet season, D2 = second dry season, W2 = second wet season). Different shapes and colors represent different land uses, and lines represent clustering identified from the analysis. Each locality consisted of three transects within each land use, with 11 traps in each transect, and these were each sampled monthly. Data presented are summed across all transects in each locality within a season. Cluster analysis: R = 0.8085, $P = 0.001$.

Fig. 2. A–C and D–F represent mean (± SE) number of butterflies collected and species richness, respectively, per land use, locality and season. Each locality consisted of three transects within each land use, with 11 traps in each transect, and these were each sampled monthly. Number of individuals and number of species across the traps within a transect were summed on a monthly basis. Data are $\log_{10}(x + 1)$ transformed to show patterns of abundance and richness for sugarcane and urban areas, and to match the log-link function in the negative binomial generalized linear mixed model.

Fig. 3. Whittaker plots of each land use by month, in which species were ranked according to their individual abundances and scaled using proportional abundance (number of individuals of a particular species / total number of individuals). Each locality consisted of three transects within each land use, with 11 traps in each transect, and these were each sampled monthly. Data presented are summed across all transects and localities within a month. Acronyms represent particularly dominant species at a particular time and locality and include *Opsiphanes cassina* (OCA), *Mnasilus allubita* (MNA), *Morpho helenor* (MOH),

Pareuptychia metaleuca (PAM), *Caligo illioneus* (CAL), *Magneuptychia libye* (MAL), *Taygetis laches* (TAL), *Glutophrissa drusilla* (GLD), *Magneuptychia ocypete* (MAO), *Historis acheronta* (HIA), *Vehilius celeus* (VEC), *Chloreuptychia agatha* (CHA) and *Caligo teucer* (CAT).

Fig. 4. A–C and D–F represent mean (± SE) Simpson indices of evenness and diversity, respectively, across land use, locality and season. Each locality consisted of three transects within each land use, with 11 traps in each transect, and these were each sampled monthly. Data presented are summed across all traps within a transect in each locality on a monthly basis.