

Butterfly (Papilionoidea and Hesperioidea) rapid assessment of a coastal countryside in El Salvador

Authors: Bonebrake, Timothy C. , and Sorto, Rubén

Source: Tropical Conservation Science, 2(1) : 34-51

Published By: SAGE Publishing

URL: <https://doi.org/10.1177/194008290900200106>

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Research Article

Butterfly (Papilionoidea and Hesperioidea) rapid assessment of a coastal countryside in El Salvador

Timothy C. Bonebrake¹ and Rubén Sorto²

¹Stanford University, Center for Conservation Biology, Dept. of Biology, Stanford, CA 94305-5020. Email: tcbone@stanford.edu

²SalvaNATURA, Conservation Science Program, 33 Ave. Sur. #640. Colonia Flor Blanca, San Salvador, El Salvador, C.A. Email: rubensorto3@yahoo.com

Abstract

Conservation organizations often must rely on data collected quickly and cheaply to make informed decisions in unstudied regions. Butterflies represent an opportunity in this respect, in that many species can typically be sampled and identified in a short time and provide an indication of habitat or conservation value as well. During nine days of sampling in June 2008, we found and identified 84 butterfly species and 1,856 butterfly individuals at Playa El Icacal, Department of La Unión, El Salvador, using transect counts. Through species richness estimators and a ratio extrapolation based on a list of species expected to be found onsite, we sampled 40-60% of the butterfly community present. Species richness at the site is estimated to be between 100 and 200 species. Sites with small patches of dry forest (La Bocana and La Laguna) had higher species richness than sites without dry forest (Hacienda Casco, El Manglar, and El Esteron). While two weeks is not enough time to fully document the butterfly community in 20 km² of neotropical coastal countryside, we were able to provide a valuable estimate of species richness and provide some information as to which areas in the region hold the most conservation value. We suggest using a list of widespread species with modified habitat associations for use as an inventory index for ratio extrapolation and discuss specific guidelines for future butterfly rapid assessments in Mesoamerica.

Keywords: Rapid evaluation, inventory, Lepidoptera, Central America

Resumen

Las organizaciones para la conservación a menudo deben depender de datos obtenidos de manera rápida, confiable y con presupuestos bajos, para la toma de decisiones orientadas en brindar información de las regiones no estudiadas. Las mariposas presentan una oportunidad en este sentido ya que muchas especies pueden ser observadas e identificadas en un período corto de tiempo, y revelarnos el estado de conservación los hábitats. Durante nueve días de muestreo en Junio 2008, observamos, Colectamos e identificamos 84 especies de mariposas de 1,856 individuos localizados en Playa El Icacal, Departamento de La Unión, El Salvador, usando una variedad de técnicas de muestreo incluidas las trampas Van Someren – Rydon con fruta fermentada, redes de mano, fotos, y la observación directa. Encontramos aproximadamente de un 40 a 60% de la actual comunidad de mariposas sobre la una base de riqueza de especies y un índice de las especies que se espera encontrar en sitio. La riqueza de especies en el lugar se estima entre 100 y 200 especies. Los Sitios de muestreo presentan pequeños parches de bosque seco, en los sitios (La Bocana y La Laguna) se reporto una mayor riqueza de especies que los en los sitios (El Casco de la Hacienda, El Manglar, y El Esteron). Que en su mayoría son pastizales. Aunque dos semanas no es tiempo suficiente para documentar completamente a las mariposas de una comunidad neotropical, en este caso unos 20 km² de la planicie aluvial costera del departamento de La Union, hemos sido capaces de proporcionar una valiosa estimación de la riqueza de especies, además de también dar algunas indicaciones en cuanto a que zonas de la región estudiada presentan mayor valor para la conservación. Asimismo proporcionamos una amplia lista de especies asociadas a los hábitats modificados para su uso como un índice en los inventarios, aparte de de proporcionar directrices específicas para el futuro de las evaluaciones rápidas de mariposas en Mesoamérica.

Palabras clave: Evaluación rápida, inventario, Lepidoptera, Centroamérica

Received: 6 December 2008; Accepted: 10 February 2009, Published: 23 March, 2009

Copyright: © Timothy C. Bonebrake and Rubén Sorto. This is an open access paper. We use the Creative Commons Attribution 3.0 license <http://creativecommons.org/licenses/by/3.0/> - The license permits any user to download, print out, extract, archive, and distribute the article, so long as appropriate credit is given to the authors and source of the work. The license ensures that the published article will be as widely available as possible and that the article can be included in any scientific archive. Open Access authors retain the copyrights of their papers. Open access is a property of individual works, not necessarily journals or publishers.

Cite this paper as: Bonebrake, T. C. and Sorto, R. 2009. Butterfly (Papilionoidea and Hesperioidea) rapid assessment of a coastal countryside in El Salvador. *Tropical Conservation Science* Vol.2 (1):34-51. Available online: www.tropicalconservationscience.org

Introduction

Tropical biologists face particularly great conservation challenges under the mounting threats of anthropogenic disturbance to biodiversity. To fully inventory diversity in tropical environments requires nearly impossible levels of time and effort [1]. Insects are a perfect example of these challenges. Worldwide species estimates range anywhere from 5-30 million [2] and species richness reaches its height in the tropics. Furthermore, even though insects make up the majority of animal species, they remain mostly undiscovered and are frequently omitted from conservation assessments [3-5].

In a rapid conservation assessment one method frequently employed by biologists to avoid the logistically impossible task of sampling an entire community, is that of indicator species which serve as a proxy for overall biodiversity [6]. Several insect taxa have been examined for utility as indicators for the state of environmental, ecological, and biodiversity of various ecosystems at multiple spatial scales (see [7] for review). Butterflies are often used as bioindicators of ecosystem health and as surrogates for overall biodiversity [8]. Sensitivity to changes in microclimate and habitat make them particularly good indicators for monitoring of natural areas undergoing change [9, 10]. As with any indicator taxa, the relationship between butterfly diversity and the diversity of other species is imperfect (for examples see [11-13]). However, butterflies have great potential as indicators for use in conservation efforts as their taxonomy, distributions, and natural history are better described than for any other insect taxa [14].

The appeal of using indicator taxa is one of logistics. By focusing on one particular set of species in a location rather than all of the species, considerable time and money (resources that can be extremely limited) can be saved. Even when focusing on indicator taxa, however, time and money are still typically insufficient to sample a given community [15]. With respect to butterflies then, how much sampling effort is required for an adequate assessment of a butterfly community? Can the conservation value of sites and habitats be distinguished from one another given short sampling periods?

In this study we sampled butterflies in five different sites consisting of different habitats (mixtures of dry forest, pasture, and mangrove) at Playa El Icacal in the Department of La Unión, El Salvador. We compared the butterfly communities and species richness at the different sites and assessed the extent to which we were able to inventory the species present at Playa El Icacal completely. We used an integrated approach to butterfly sampling including multiple habitats, assessment of sampling effort, and multiple data collection techniques. Such an approach is essential for tropical conservation programs aimed at Lepidoptera [16]. We then demonstrated the potential utility of studies undertaken with limited sampling time and concluded that while not

ideal, studies of low sampling effort can provide comparable diversity estimates and even give some indication as to which sites in a region have superior or inferior habitat qualities with respect to butterflies and potentially to insects or biodiversity more generally.

Methods

Study site and organisms

Playa El Icacal is a coastal countryside community in the department of La Unión, El Salvador. We sampled five sites within Playa El Icacal (Figs. 1 and 2). La Bocana consists of a dry forest habitat and also a large open pasture. La Laguna also has dry forest and a pasture dotted with shrubs and isolated trees. Hacienda Casco is a roadside habitat with a matrix of pasture, shrubs, and small trees. El Manglar is a roadside transect that is surrounded by a mangrove forest and cattle pasture on either side. Finally, El Esteron is a large pasture with isolated trees and shrubs that is directly adjacent to the western estuary of El Icacal.

We sampled all butterflies of Papilionoidea and Hesperioidea. Identification of species within the Nymphalidae, Pieridae, Papilionidae, and Riodininae followed DeVries [17, 18] and the identification of species within Lycaenidae and Hesperidae followed Glassberg [19]. Here we use the nomenclature of Lamas [20].

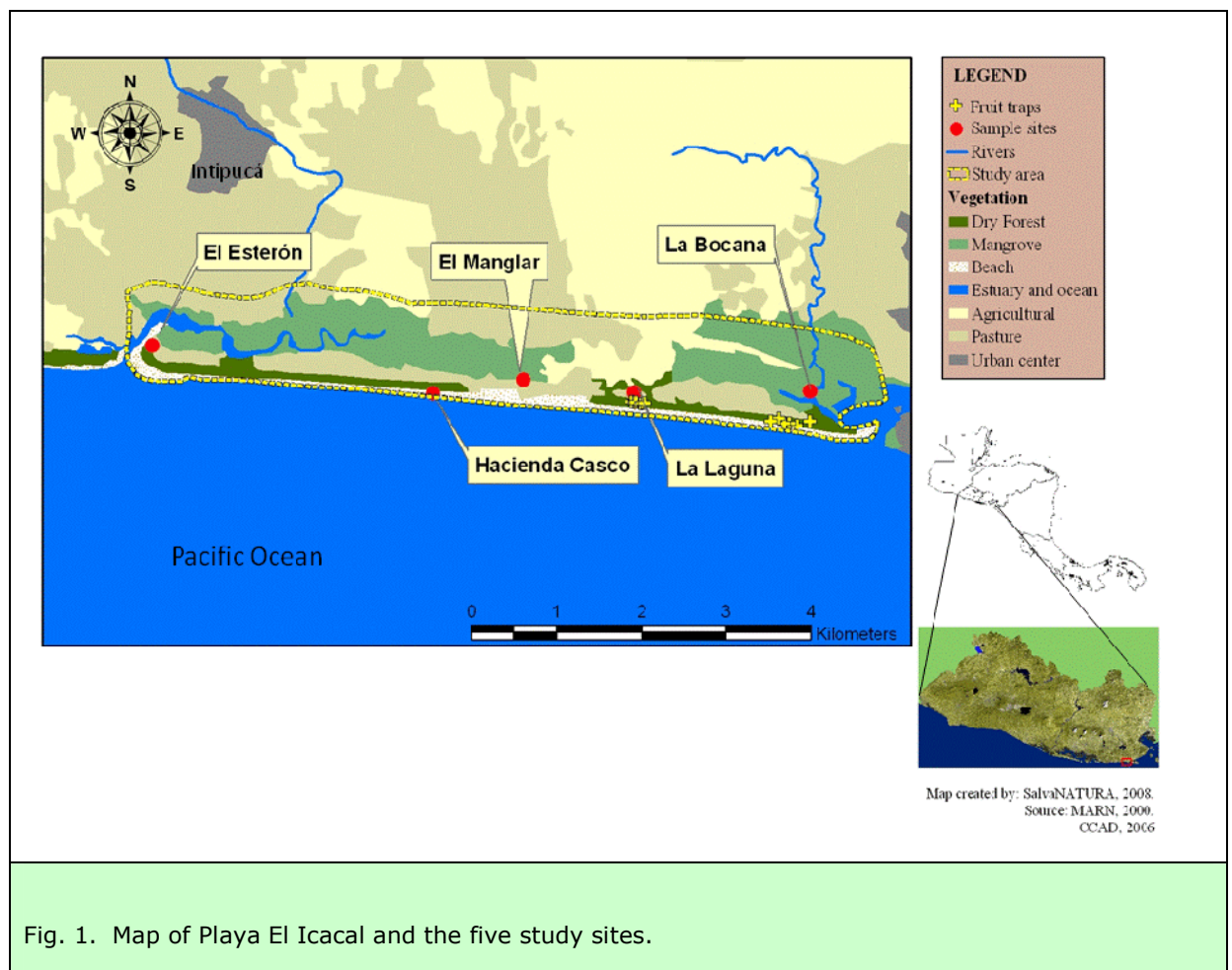


Fig. 1. Map of Playa El Icacal and the five study sites.

Sampling protocol

Frugivorous butterflies were trapped using cylindrical Van Someren-Ryndon traps baited with rotting bananas and beer [21]. Six traps were placed in each of the two sites with forest cover (La Bocana and La Laguna) approximately 2-3 meters off the ground. Suitable places for fruit-baited traps in the other three sites (Casco, El Esteron, and El Manglar) were not available or too logistically difficult for set up (e.g., mangroves in El Manglar were difficult to access and maneuver within, which complicated efforts to establish fruit-baited traps). Traps were checked daily for seven days (from June 17 to June 23) for a total of approximately 2,000 trap hours (12 traps used for seven days).

One transect for each site was constructed based on available trails and focused on prominent nectar sources, mud puddles, and other resource-rich locations within each site [22,23]. While there was no specified distance for each of the transects, we contained each of the sites within an area of about 250 m². We instead focused on time, and each transect was sampled at least every other day and for at least one hour.

Collection occurred during hours of weather favorable for butterfly flight (sunny and negligible wind) and was undertaken solely by the authors, both sufficiently familiar with Central American butterflies to identify them with only few errors (though surely we made them!). We noted all butterflies seen during each transect. Butterflies requiring identification were either photographed or captured with a hand net and examined upon returning from the field. Nearly all specimens taken from the field were identifiable with the exception of approximately 10 butterflies (mostly Hesperidae) that were too damaged for accurate identification. Butterflies that were too fast or too far to reliably identify were not counted. Specimens were deposited at the Museum for Natural History of El Salvador and digital photographs were taken to a photographic database kept and maintained by SalvaNATURA.

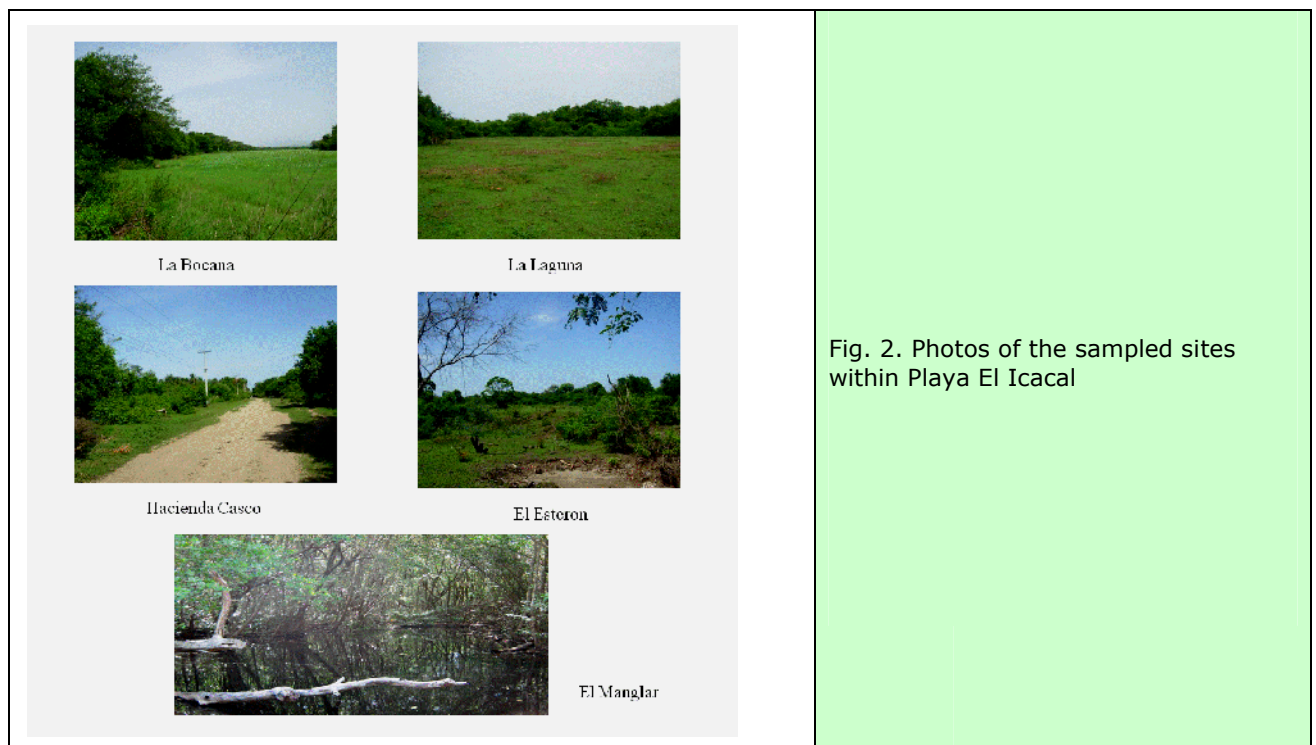


Fig. 2. Photos of the sampled sites within Playa El Icacal

Species richness and diversity analysis

Effort and sampling efficiency were assessed by calculating species richness estimators using EstimateS software [24] based on individual-based species accumulation curves [25]. Species richness estimates were compared between sites using a rarefaction curve in EcoSim [26].

We generated a list of species we would expect to find at the site based on Thomas [27] which classifies 74 species within the Nymphalidae, Pieridae, and Papilionidae of Costa Rica as being widespread (ranging throughout Central America south to at least Brazil) and found in modified habitats. For this reason we expected to find most, if not all, of these species at Playa El Icacal. We could then extrapolate to estimate species richness using a taxonomic hierarchical ratio [28] that assumes the focal taxa (in this case Nymphalidae, Pieridae, and Papilionidae of broad distribution and disturbed habitats) respond to collection time in the same way as that of the target taxa (in this case the entire butterfly fauna). Therefore, we estimated species richness in this way by using the relationship that $\# \text{ species found} / \# \text{ of species total} = \# \text{ of species found within the index} / \# \text{ of species total in the index}$. The Nymphalidae, Pieridae, and Papilionidae represent the best known and most visible of the butterflies and so sampling is often biased in favor of these species [29]. Additionally, good field guides and natural history information are generally lacking for many tropical lycaenid and hesperid species. Due to this bias, the ratio extrapolation may be an underestimate of the species present.

The above methods describe estimation of species richness of the study area and within sites. These methods ignore the evenness of communities. We therefore additionally calculated Fisher's alpha [30] for each of the sites which combines both richness and evenness attributes of the communities [31]. We calculated Fisher's alpha in R [32] using the VEGAN package [33]. Given the small sampling period we were unable to effectively examine quantitatively diversity patterns within and between Papilionoidea and Hesperioidea and instead focused on the butterfly community as a whole.

Community and species composition analysis

We performed a community-level analysis using nonmetric multidimensional scaling (NMDS) [34]. The ordination was based on a Bray-Curtis dissimilarity matrix of ecological distance [35]. We performed the NMDS in SYSTAT 12.0 (SYSTAT Software, Inc. 2007).

Table 1 Species richness estimators of Playa El Icacal. The ACE is the "Abundance-based Coverage Estimator" and the ICE is the "Incidence-based Coverage Estimator". The Chao 1 and Chao 2 are estimators based on Chao [45], and Jack 1 and Jack 2 are respectively the first and second-order Jackknife richness estimators. For a review of these and other species richness estimators see Magurran [31].

Species Richness	
Estimator	(Mean among runs)
ACE	100
ICE	122
Chao 1	97
Chao 2	138
Jack 1	113
Jack 2	132

Results

Species sampled

We sampled 84 butterfly species and 1,856 butterfly individuals at Playa El Icacal in nine days over a total of 58 collecting/netting hours along the transects (Appendix 1). We sampled five species and 14 individuals in the baited fruit traps (1 *Zaretis ellops*, 4 *Hamadryas februa*, 1 *Hamadryas guatemalena*, 6 *Temenis laothoe*, and 1 *Opsiphanes tamarindi*). Three of these (*Z. ellops*, *T. laothoe*, and *O. tamarindi*) were not recorded by any other method.

State of the inventory and species richness

We calculated six estimators of species richness based on the data (Table 1). The largest estimate of species richness at Playa El Icacal over all five sites was 138 using a Chao 2 estimate. This estimate would suggest that the 84 species we detected represented 61% of the species richness present during our visit. Chao 1, the least conservative estimate of sampling effort (and lowest estimator of species richness) suggested that 87% of the present butterfly fauna were detected.

Of the 84 species we found, 31 were defined by Thomas [27] as widespread and of modified habitats (Appendix 2). We therefore sampled 42% (31/74) of the species that we expected to find. Using the ratio extrapolation ($84/x=.42$), this would suggest that there are approximately 200 species of butterfly (Papilionoidea and Hesperioidea) at Playa El Icacal.

Habitat and site comparison

Based on rarefaction curves, the two sites with tracts of dry forest (La Bocana and La Laguna) had higher species richness than other sites (Fig. 3). The 95% confidence intervals for species richness at 200 individuals of both La Laguna (34-41 species) and La Bocana (33-42 species) have statistically significant higher levels than El Esteron (26-30 species; Fig. 3) but not significantly higher than El Manglar (31-33 species) and Hacienda Casco (29-34 species).

Diversity and community analysis

Fisher's alpha for the sites was highest in La Bocana (13.01) and La Laguna (11.74) mirroring the pattern found in species richness. El Manglar (10.97) and Hacienda Casco (10.76) had the next highest diversity with El Esteron (9.32) containing the lowest estimate of diversity. The NMDS showed clustering of La Bocana and La Laguna as well as clustering of Hacienda Casco and El Esteron (Fig. 4). El Manglar fell out as a unique assemblage, dissimilar to the four other sites (Fig. 4).

Discussion

Sampling effort and inventory completeness

In nine days of sampling we sampled approximately 40-60% of the estimated butterfly fauna at Playa El Icacal. Though this is a small amount of time for sampling such a diverse community we were able to find significant differences between sampled sites in addition to being able to provide an estimate of the species richness in the area. Had we sampled even a day or two less than the nine days we sampled, site differences might have been difficult to detect; La Bocana and El Esteron, for example, only differed significantly after the last 20-40 individuals sampled in rarefaction (Fig. 3). Based on the community-level analysis we were also able to identify El Manglar as a unique site even though species richness was lower than La Laguna and La Bocana (Fig. 4).

Certainly more time spent sampling would have improved both species richness estimates of the area as well as site differences in the butterfly community. Another nine days would have shrunk the confidence intervals, and sampling throughout the season (approximately May-November) would have done so even more. Another strategic approach would have been to sample again for another 7-9 days later in the season to better account for seasonality effects. Nevertheless, we

were restricted here to nine days but were still able to provide a reasonable and valuable picture of the butterfly diversity in the area.

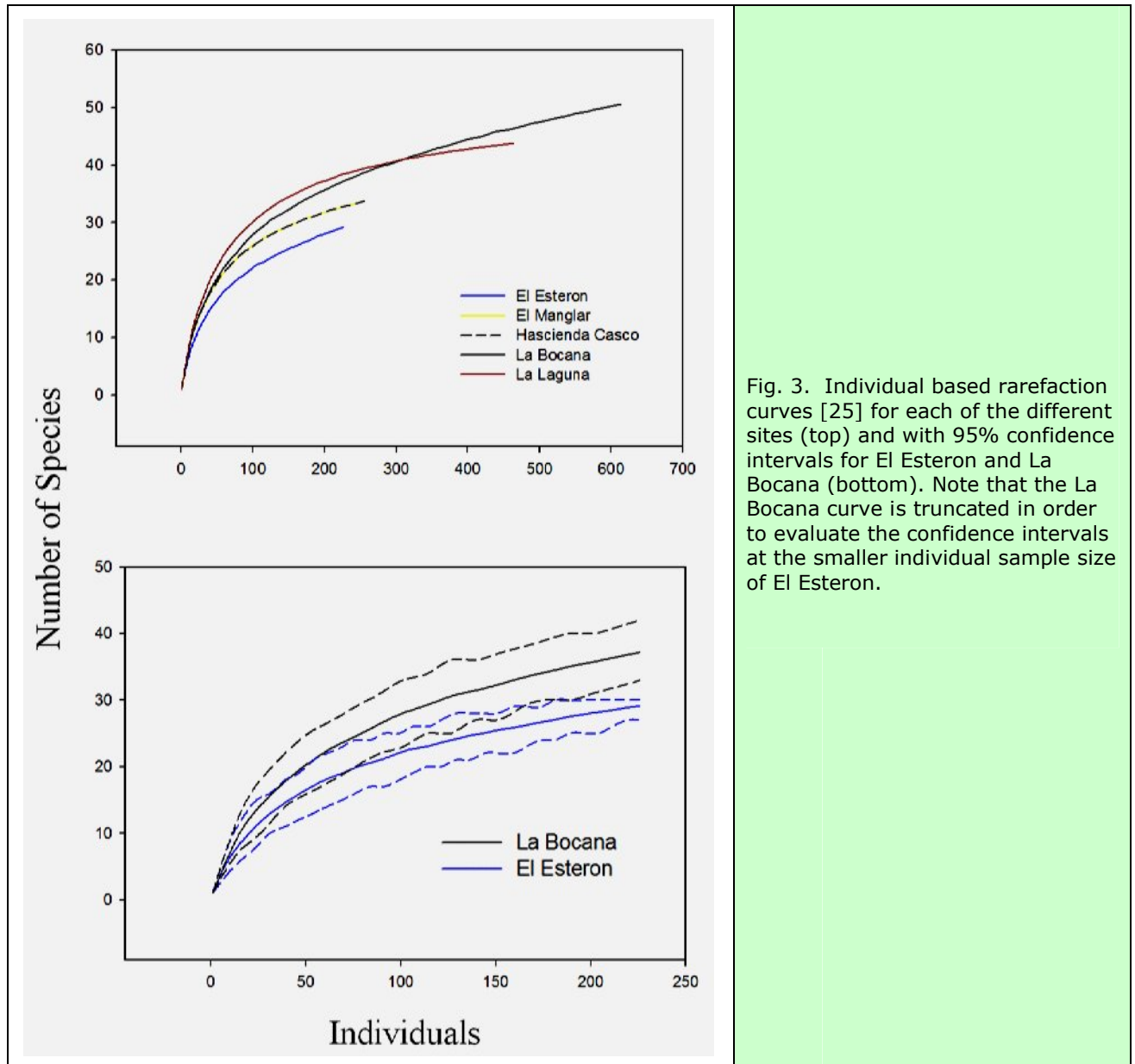


Fig. 3. Individual based rarefaction curves [25] for each of the different sites (top) and with 95% confidence intervals for El Esteron and La Bocana (bottom). Note that the La Bocana curve is truncated in order to evaluate the confidence intervals at the smaller individual sample size of El Esteron.

Evaluation of habitats and suitable sampling methods

Taken together these results corroborate a growing consensus that human dominated landscapes can often support diverse assemblages of butterflies [23, 36, 37]. This is not to say that natural habitat is unimportant nor do we imply that the butterfly community sampled here is equivalent to a community within a large forest preserve. The data show that the sites with some amount of forest (La Bocana and La Laguna) had the highest diversity and provided habitat for the most species of butterflies. Other insect species have not been sampled at Playa El Icacal but in the

absence of such data, we could use this assessment as a biodiversity indicator and predict insect species patterns to follow similar patterns as those found in the butterflies. Though correlations between butterflies and other insects are decidedly imperfect, in the absence of more complete insect survey data we suspect that La Bocana and La Laguna are likely to be important sites for insect conservation in the Playa El Icaal region. Certainly, further surveys of insect communities at Playa El Icaal to test these correlations and relationships in an adaptive management context would be ideal [38].

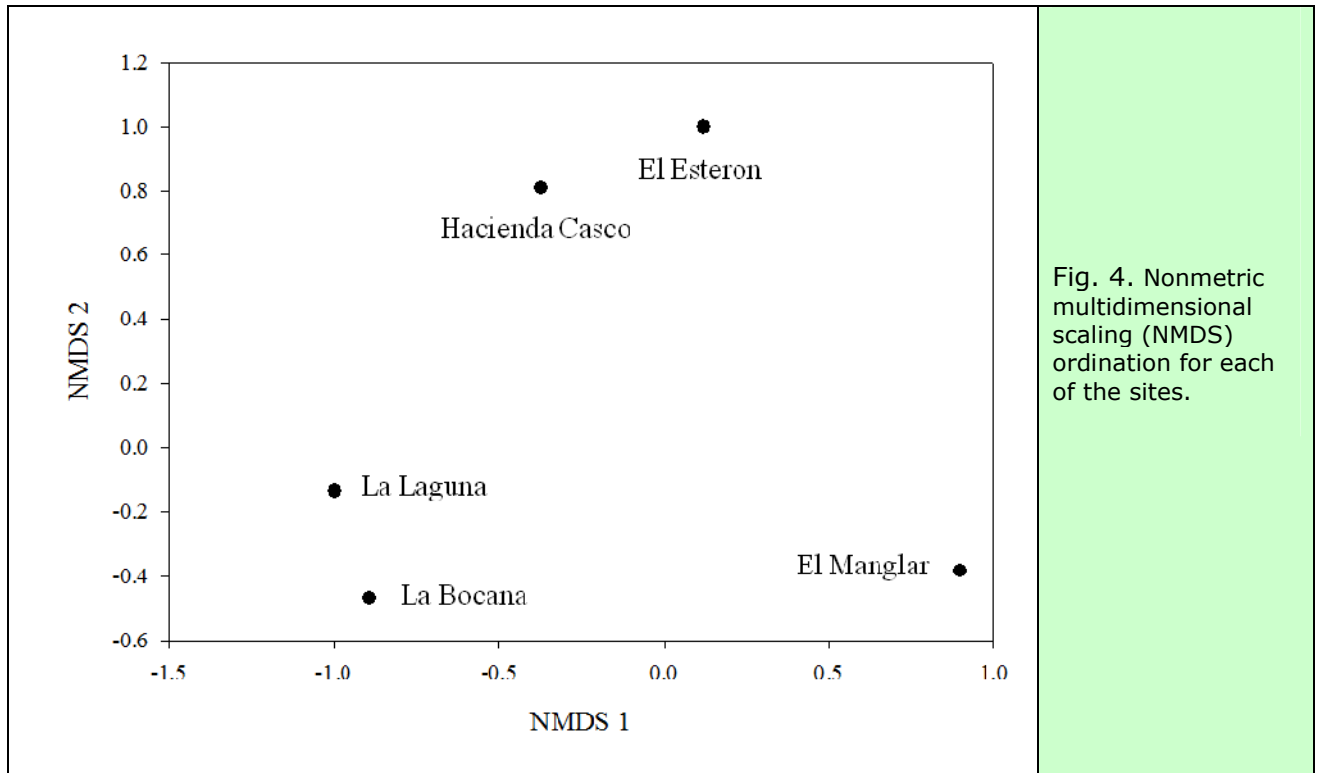


Fig. 4. Nonmetric multidimensional scaling (NMDS) ordination for each of the sites.

Families and subfamilies of butterflies tend to have different habitat requirements and it can be informative to examine within taxa patterns. For example, *Zaretis ellops* of the Charaxinae subfamily is associated with undisturbed habitat [27], and the capture of this individual only at La Bocana highlights the importance of the dry forest habitat at Playa El Icaal. Also, we caught one individual of *Opsiphanes tamarindi* (Brassoliniinae) in La Bocana, another forest-associated species and the only representative of the Brassoliniinae. We found no individuals of the Ithomiinae subfamily. Ithomiinae have been targeted as useful indicator taxa for butterflies as they tend to have very forest-specific habitat requirements [39]. It is unclear whether their absence at Playa El Icaal is a result of limited sampling given the high seasonality of the Ithomiinae [40] or if it is due to the lack of good forest habitat. El Manglar was distinguished in the NMDS ordination as being unique to the other sites (Fig. 4). Compositionally the site was unique in a couple of ways including large numbers of *Danaus* individuals as well as a more diverse lycaenid fauna (Appendix 1).

Baited fruit traps are frequently cited as a tool for rapid assessment of neotropical butterfly communities [41]. Using these traps we found three species (*Z. ellops*, *O. tamarindi*, and *T.*

laothoe) that we would have otherwise not seen. However, only a very small fraction (6%) of the species was represented by the fruit-baited trap captures with only seven trapping days, though additional traps might have also improved capture rates. For rapid assessments of only a few months and in habitats other than rainforest, it is advisable to supplement fruit-baited trapping with hand-net capture.

Diversity estimates: uncertainty and assumptions

A more complete survey of an area such as Playa El Icacal would require more sampling time, as the seasonality of butterflies is one factor likely to complicate sampling efforts. For example, dry forest habitats, such as those found at Playa El Icacal, are often characterized by a succession of butterfly assemblages throughout the year [17]. Not only do dry season and wet season assemblages differ from one another, but also the composition of butterflies at the beginning of the wet season typically differs from the composition of species mid-way through the wet season.

To illustrate this point, consider a similar butterfly inventory undertaken in comparable habitats (though baited fruit traps were not used) in July and in December of 2006 at nearby Salamar, Department of Usulután, El Salvador, about 15 kilometers west of El Icacal [42]. After nine days in Salamar, 34 species were found. Most of these species were from the families Nymphalidae, Pieridae, and Papilionidae. There were 20 species shared between the Salamar and the present surveys. We did not find several species that we expected to find, though they were found by Mendéz and Funes [42]. These included *Siproeta stelenes*, *Heliconius hecale*, and *Eueides isabella*. Also interestingly, we did not find *Anartia fatima* until the fourth day of sampling despite this species being one of the most commonly seen butterflies in Central America [17]. These species are often very common in most Mesoamerican habitats and their absence from our sampling is more likely indicative of seasonal differences than an actual absence of these species at Playa El Icacal.

The species richness estimators are based on the assumption that the community being sampled is present at all times of sampling. But, given the seasonality of the butterflies, many species may not have been flying during the sampling period. The ratio extrapolation based on the expected species list is reflective of all expected butterflies in a given habitat rather than solely of the present community at the time of sampling. It is therefore possibly more resistant to seasonality problems than the species richness estimators (ICE, Chao 1, Chao2, Jack 1, etc.). This could explain the 20% (or greater) difference in the completeness estimates for the inventory and suggests that in short time periods that don't reflect a community's seasonality, the ratio extrapolation approach may be more robust to such problems.

The ratio extrapolation approach has its own assumptions and uncertainties however. First, it assumes a strong correlation between finding the focal species and the target species (see Methods and Materials section). In this instance it seems likely that the focal species (broadly distributed species of disturbed habitat within Nymphalidae, Pieridae, and Papilionidae) are easier to find than the non-focal species given the detection bias towards the focal species. Therefore, it is quite possible that 200 species is an underestimate. On the other hand, it is also possible that a lack of correlation between the non-focal and focal species exists not because of detection bias but instead because of "presence" bias. It is possible that non-focal species are distributed differently than focal species and these groups are simply uncorrelated with one another. This could then overestimate the number of species, as a large percentage of the non-focal species predicted to be present at the site would simply not be there. Given these uncertainties and assumptions, we feel that 200 species is a good first approximation of the number of species present at Playa El Icacal but also predict the actual number of species is likely to be more or less based on the accuracy of the focal and non-focal taxa correlation.

Implications for conservation

There are an estimated 540 species of butterflies (Papilionoidea and Hesperioidea) at El Imposible, El Salvador's largest national park, which consists of tracts (about 9,000 acres) of tropical dry and moist forest covering a large altitudinal range from near sea level to over 1,400 m a.s.l. [43]. We certainly would not expect to find comparable numbers of species at a site as small as Playa El Icacal, without moist tropical forest and a large altitudinal range. However, the 100-200 butterfly species that we did estimate are impressive given the lower variability in habitat and greater fragmentation of native habitat (Fig. 5).



Fig. 5. A sample of the butterfly species found at Playa El Icacal. *Arawacus sito* (top left), *Dryas iulia* (top right), *Heraclides cresphontes* (bottom left), and *Timochares trifasciata* (bottom right). Photos by T. Bonebrake and R. Sorto.

There are a variety of techniques and approaches to monitoring of neotropical butterfly communities [see 16]. In this study, we provide further guidelines with special emphasis on time-limited rapid assessments:

- Multiple data collection techniques (including baited traps, hand-net captures, visual censuses, and digital photography) enhance the ability to find species.
- Species accumulation curves and richness estimators can provide not only useful information about the number of species in a region, but also an estimate of the completeness of an assessment. However, seasonal changes can result in an underestimate of species richness.
- Using common species lists, or expected species list, as an index for ratio extrapolation can be another approach to estimating assessment completeness (and species richness). However, the accuracy of this extrapolation is dependent upon the correlation between focal (butterflies on the list) and target species (all butterflies) which introduces error into estimates.
- We have provided a list based on designations of Costa Rican butterflies by Thomas [27], which could be used as a list of butterflies expected to be found in most Mesoamerican locations with even small amounts of suitable, non-paved habitat.
- Comparing diversity between habitats is very sensitive to sample size, but using rarefaction curves allows for accurate comparisons between habitats even when sample sizes are low or disparate.
- Community-level analysis through ordination can be a useful means of describing species composition and distinguishing unique community assemblages.

Time allowing, exhaustive and extensive sampling, both temporally and spatially, is the only way to understand and document a butterfly community fully, particularly in such complicated ecosystems as tropical forests [44]. Under resource-limited circumstances this is rarely possible. However, important and accurate information can be attained in a short time when careful attention is paid to the uncertainty and flaws inherent in such time-limited sampling efforts. Furthermore, this is the only survey of any insect community undertaken at Playa El Icacal to date. While the utility of butterflies as indicators of biodiversity continues to be tested and refined, we feel that the results presented here will helpfully guide conservation efforts in this area. We also hope that perhaps this study will inspire a more thorough investigation of the insect and ultimately the ecological community of this Salvadoran coastal countryside and others like it.

Acknowledgements

We are grateful for the support of this research by SalvaNATURA. We thank the National Science Foundation (OISE-0832204) for additional funding support. Comments and suggestions from C. Boggs, P. Ehrlich, O. Komar, E. Pringle, and two anonymous reviewers improved the manuscript by an order of magnitude. V. Henríquez helped create the Playa Icacal map. K. Lara masterfully organized and executed field accommodations and facilitated the collection permit process. We thank the Ministerio de Medio Ambiente y Recursos Naturales (MARN) in El Salvador for granting the permits.

References

- [1] Lawton, J.H., Bignell, D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S. and Watt, A.D. 1998. Biodiversity inventories, indicator taxa, and effects of habitat modification in tropical forest. *Nature* 391: 72-76.
- [2] Godfray, H.C.J., Lewis, O.T. and Memmott, J. 1999. Studying insect diversity in the tropics. *Philosophical Transactions of the Royal Society of London B* 354: 1811-1824.
- [3] Meyers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853-858.
- [4] Clark, J.A., and May, R.M. 2002. Taxonomic bias in conservation research. *Science* 297: 191-192.
- [5] Leather, S.R., Basset, Y. and Hawkins, B.A. 2008. Insect conservation: finding the way forward. *Insect Conservation and Diversity* 1: 67-69.
- [6] Kerr, J.T., Sugar, A. and Packer, L. 2000. Indicator taxa, rapid biodiversity assessment, and nestedness in an endangered ecosystem. *Conservation Biology* 14: 1726-1734.
- [7] McGeoch, M.A. 1998. The selection, testing, and application of terrestrial insects as bioindicators. *Biological Reviews* 73: 181-201.
- [8] Sisk, T.D., Launer, A.E., Switky, K.R., and Ehrlich, P.R. 1994 Identifying extinction threats: global analyses of the distribution and the expansion of the human enterprise. *Bioscience* 44: 592-604.
- [9] Erhardt, A. 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology* 22: 849-862.
- [10] Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2: 203-217.
- [11] Singer, M.C. and Ehrlich, P.R. 1991. Host specialization of satyrine butterflies, and their response to habitat fragmentation in Trinidad. *Journal of Research on the Lepidoptera* 30: 248-256.
- [12] Ricketts, T.H., Daily, G.C. and Ehrlich, P.R. 2002. Does butterfly diversity predict moth diversity? *Biological Conservation* 101: 361-370.
- [13] Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, V., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I., and Tschardt, T. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications* 14: 1321-1333.
- [14] Brown, K.S. 1997. Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. *Journal of Insect Conservation* 1: 25-42.
- [15] Gardner, T.A., Barlow, J., Araujo, I.S., Ávila-Pires, T.S., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., and Peres, C.A. 2008. The cost-effectiveness of biodiversity surveys in tropical forests. *Ecology Letters* 11:139-150.
- [16] Sparrow, H. R., T. D. Sisk, P. R. Ehrlich, and D. D. Murphy. 1994. Techniques and guidelines for monitoring neotropical butterflies. *Conservation Biology* 8: 800-809.
- [17] DeVries, P.J. 1987. The Butterflies of Costa Rica and their Natural History. Vol. 1. Papilionidae, Pieridae, and Nymphalidae. Princeton University Press, Princeton.
- [18] DeVries, P.J. 1997. The Butterflies of Costa Rica and their Natural History. Vol. 2. Riodinidae. Princeton University Press, Princeton.
- [19] Glassberg, J. 2007. A Swift Guide to the Butterflies of Mexico and Central America. Sunstreak Books.

- [20] Lamas, G. 2004. Atlas of Neotropical Lepidoptera. Association of Tropical Lepidoptera, Scientific Publishers.
- [21] Hughes, J. B., Daily, G.C., and Ehrlich, P.R. 1998. Use of fruit bait traps for monitoring of butterflies (Lepidoptera: Nymphalidae). *Revista de Biología Tropical* 46: 697-704.
- [22] Raguso, R.A., and Llorente, J. 1990. The butterflies of the Tuxtla Mts., Veracruz, Mexico revisited: species richness and habitat disturbance. *Journal of Research on the Lepidoptera* 29:105-133.
- [23] Horner-Devine, M. C., Daily, G.C., Ehrlich, P.R., and Boggs, C.L. 2003. Countryside biogeography of tropical butterflies. *Conservation Biology* 17:168-177.
- [24] Colwell R.K . 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. User's guide and application published at: <http://purl.oclc.org/estimates>
- [25] Gotelli, N.J., and Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379-391.
- [26] Gotelli, N.J. and Entsminger, G.L. 2000. EcoSim: Null models software for ecology. Version 5.0. Acquired Intelligence Inc. & Kesey-Bear. <http://homepages.together.net/~gentsmin/ecosim.htm>.
- [27] Thomas, C.D. 1991. Habitat use and geographic range of butterflies from the wet lowlands of Costa Rica. *Biological Conservation* 55: 269-282.
- [28] Colwell, R.K. and Coddington, J.A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* 345: 108-118.
- [29] Caldas, A. and Robbins, R.K. 2003. Modified Pollard transects for assessing tropical butterfly abundance and diversity. *Biological Conservation* 11: 211-219.
- [30] Fisher, R.A., Corbet, A.S., and Williams, C.B. 1943. The relation between number of individuals and the number of species in a random sample of an animal population. *Journal of Animal Ecology* 12:42-58.
- [31] Magurran, A.E. 2004. Measuring Biological Diversity. Blackwell, Oxford.
- [32] R Core Development Team. 2005. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Australia.
- [33] Oksanen, J., Kindt, R., and O'hara, R. 2005. Vegan: community ecology package. Online at: <http://vegan.r-forge.r-project.org/>
- [34] Kruskal, J.B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115-129.
- [35] Faith, D.P., Minchin, P.R., and Belbin, L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57-68.
- [36] Ohwaki, A., Nakamura, K., and Tanabe, S. 2007. Butterfly assemblages in a traditional agricultural landscape: importance of secondary forests for conserving diversity, life history specialists and endemics. *Biodiversity and Conservation* 16: 1521-1539.
- [37] Barlow, J., Araujo, I.S., Overal, W.L., Gardner, T.A., Mendes, F.S., Lake, I.R., and C. Peres. 2008. Diversity and composition of fruit-feeding butterflies in a tropical *Eucalyptus* plantation. *Biodiversity and Conservation* 17: 1089-1104.
- [38] Lindenmayer, D.B., Margules, C.R., and Botkin, D.B. 2000. Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology* 14: 941-950.
- [39] Beccaloni, G.W., and Gaston, K.J. 1995. Predicting the species richness of neotropical forest butterflies- Ithomiinae (Lepidoptera, Nymphalidae) as indicators. *Biological Conservation* 71: 77-86.
- [40] Brown, KS Jr., and Freitas, A.V.L. 2000. Atlantic forest butterflies: Indicators for landscape conservation. *Biotropica* 32: 934-956.
- [41] Daily, G. C., and Ehrlich, P.R. 1995. Preservation of biodiversity in small rain forest patches: rapid evaluations using butterfly trapping. *Biodiversity and Conservation* 4:35-55.
- [42] Mendéz, M., and C. Funes. 2007. Inventario de Mariposas en Salamar, Colinas de Jucuarán, Departamento de Usulután, El Salvador. SalvaNATURA Informe de Consultoría.

- [43]** Serrano, F. 2003. Las mariposas. In J.M. Alvarez & O. Komar (Ed). El Parque Nacional El Imposible y su vida silvestre. La Serie de Biodiversidad No. 2. SalvaNATURA. Pág. 123-137.
- [44]** DeVries, P.J., D. Murray, and R. Lande. 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* 62: 343-364.
- [45]** Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43: 783-791.

Appendix 1 Number of individuals sampled for each species by each site during nine days at Playa El Icacal along with species richness total from each of the sites.

*Species sampled by fruit-baited traps.

Family	Species	La Bocana	La Laguna	Hacienda Casco	El Manglar	El Esteron
Species Richness Site Total:		51	44	35	33	31
Papilionidae	<i>Battus polydamas</i>	13	7	6	6	3
	<i>Heraclides thoas</i>	4	2	2	0	0
	<i>Heraclides crephontes</i>	11	13	7	0	0
	<i>Protographium epidaus</i>	1	0	0	2	2
Pieridae	<i>Glutophrissa drusilla</i>	3	4	0	0	0
	<i>Ascia monuste</i>	34	24	0	5	8
	<i>Anteos clorinde</i>	7	0	0	1	1
	<i>Phoebis philea</i>	8	16	0	1	0
	<i>Phoebis agarithe</i>	4	4	4	0	1
	<i>Phoebis sennae</i>	34	34	20	10	20
	<i>Aphrissa boisduvalii</i>	8	10	0	0	0
	<i>Pyrisitia proterpia</i>	2	1	2	0	1
	<i>Pyrisitia nise</i>	0	0	1	0	0
	<i>Eurema mexicana</i>	15	0	0	0	0
	<i>Eurema दौरا</i>	150	79	38	30	90
	Nymphalidae	<i>Zaretis ellops*</i>	1	0	0	0
<i>Consul fabius</i>		0	1	0	0	0
<i>Libytheana carinenta</i>		0	0	4	0	4
<i>Hamadryas februa*</i>		13	6	0	4	1
<i>Hamadryas glauconome</i>		0	0	0	2	0
<i>Hamadryas guatemalena*</i>		0	2	0	0	1
<i>Marpesia petreus</i>		1	3	3	2	3
<i>Marpesia chiron</i>		1	0	0	0	0
<i>Eunica monima</i>		0	0	1	0	1
<i>Temenis laothoe*</i>		2	4	0	0	0
<i>Anartia fatima</i>		0	0	1	1	0
<i>Anartia jatrophae</i>		0	15	0	22	6
<i>Junonia evarete</i>		2	6	8	2	14
<i>Euptoieta hegesia</i>		6	9	0	4	7

**Appendix 1
continued**

Family	Species	La Bocana	La Laguna	Hacienda	El Manglar	El Esteron
	<i>Dryadula phaetusa</i>	19	9	6	0	0
	<i>Dione juno</i>	14	10	8	4	8
	<i>Dione moneta</i>	14	5	0	0	0
	<i>Agraulis vanillae</i>	13	10	6	0	7
	<i>Dryas iulia</i>	40	28	24	10	8
	<i>Heliconius charithonia</i>	44	42	30	8	14
	<i>Heliconius erato</i>	58	36	34	12	23
	<i>Chlosyne janais</i>	0	1	0	0	0
	<i>Chlosyne lacinia</i>	0	1	0	0	0
	<i>Anthanassa drusilla</i>	0	0	0	1	0
	<i>Danaus plexippus</i>	5	2	0	4	0
	<i>Danaus gilippus</i>	0	2	0	2	0
	<i>Danaus eresimus</i>	19	6	8	26	4
	<i>Opsiphanes tamarindi*</i>	1	0	0	0	0
	<i>Caligo telamonius</i>	1	1	0	0	0
	<i>Taygetis laches</i>	1	0	0	0	0
	<i>Hermeuptychia sosybius</i>	0	0	0	14	0
Riodinidae	<i>Synargis mycone</i>	3	0	1	0	1
	<i>Lasaia sula</i>	1	0	1	0	0
	<i>Melanis electron</i>	2	0	0	0	0
	<i>Melanis cephise</i>	8	0	0	0	0
	<i>Juditha molpe</i>	2	0	2	0	3
	<i>Theope eupolis</i>	5	0	0	0	0
Lycaenidae	<i>Panthiades bathildis</i>	0	0	0	1	0
	<i>Panthiades bitias</i>	1	0	0	0	0
	<i>Arawacus sito</i>	1	0	0	2	4
	<i>Hemiargus hanno</i>	0	0	5	0	0
	<i>Tmolus echion</i>	0	0	0	1	0
	<i>Strephonota tephraeus</i>	0	1	0	0	0
	<i>Brangas neora</i>	0	0	1	0	0
	<i>Cyanophrys herodotus</i>	0	0	0	0	1
	<i>Rekoa marius</i>	0	0	0	4	0
	<i>Calycopis isobea</i>	0	2	0	0	0

**Appendix 1
continued**

Family	Species	La Bocana	La Laguna	Hacienda	El Manglar	El Esteron
Hesperiidae	<i>Erynnis funeralis</i>	0	0	0	0	2
	<i>Urbanus dorantes</i>	32	19	8	8	8
	<i>Urbanus pronus</i>	6	10	3	0	0
	<i>Urbanus proteus</i>	0	8	5	2	0
	<i>Urbanus procne</i>	0	0	0	0	2
	<i>Orses cynisca</i>	1	0	0	0	0
	<i>Calpodus ethlius</i>	1	0	0	0	0
	<i>Thespius macareus</i>	1	0	0	0	0
	<i>Mylon pelopidas</i>	7	7	12	0	0
	<i>Synapte syraes</i>	2	0	0	0	0
	<i>Pyrgus oileus</i>	0	2	2	8	0
	<i>Pyrgus communis</i>	0	4	1	0	0
	<i>Astrartes anaphus</i>	0	0	1	2	0
	<i>Hylephila phyleus</i>	0	6	6	0	0
	<i>Bolla clytius</i>	0	0	0	0	1
	<i>Timochares trifasciata</i>	0	0	0	2	0
	<i>Achalarus toxeus</i>	0	8	4	0	0
	<i>Thessia jalapus</i>	18	22	2	0	0
	<i>Nyctelius nyctelius</i>	0	0	0	0	1
	<i>Antigonus erosus</i>	0	4	0	8	0
	<i>Epargyreus exadeus</i>	1	0	0	0	0
	<i>Phocides belus</i>	1	0	0	0	0

Appendix 2. A list of 74 butterflies we expected to find based on designations by Thomas [27] of widespread butterfly species often found in modified habitats. Species in bold represent species we sampled at Playa El Icacal.

Number	Expected Species	Number	Expected Species
1	Battus polydamas	18	Eurema daira
2	Heraclides thoas	19	<i>Archaeoprepona demophon</i>
3	<i>Heraclides androgeus</i>	20	<i>Archaeoprepona demophoon</i>
4	<i>Heraclides anchisiades</i>	21	<i>Siderone galanthis</i>
5	Glutophrissa drusilla	22	Consul fabius
6	Ascia monuste	23	<i>Memphis arginussa</i>
7	<i>Zerene cesonia</i>	24	<i>Memphis oenomais</i>
8	Anteos clorinde	25	<i>Memphis pithyusa</i>
9	<i>Phoebis neocypris</i>	26	<i>Doxocopa laure</i>
10	Phoebis philea	27	<i>Colobura dirce</i>
11	Phoebis agarithe	28	<i>Historis odius</i>
12	Phoebis sennae	29	<i>Historis archeronta</i>
13	<i>Aphrissa statira</i>	30	<i>Biblis hyperia</i>
14	Pyrisitia proterpia	31	Hamadryas februa
15	Pyrisitia nise	32	<i>Hamadryas feronia</i>
16	<i>Eurema albula</i>	33	<i>Hamadryas amphinome</i>
17	Eurema mexicana	34	<i>Dynamine postverta</i>
35	Marpesia petreus	57	<i>Heliconius hecale</i>
36	Marpesia chiron	58	<i>Heliconius sara</i>
37	<i>Marpesia berania</i>	59	Chlosyne lacinia
38	<i>Nica flavilla</i>	60	Anthanassa drusilla
39	<i>Catonephele numilia</i>	61	Danaus plexippus
40	<i>Diaethria clymena</i>	62	Danaus eresimus
41	<i>Adelpha cytherea</i>	63	<i>Tithorea tarricina</i>
42	<i>Adelpha iphiclus</i>	64	<i>Thyridia psidii</i>
43	<i>Adelpha naxia</i>	65	<i>Mechanitis polymnia</i>
44	<i>Hypanartia lethe</i>	66	<i>Hypothyris euclea</i>
45	<i>Siproeta stelenes</i>	67	<i>Dynastor darius</i>
46	Anartia jatrophae	68	Opsiphanes tamarindi
47	Junonia evarete	69	<i>Opsiphanes cassina</i>
48	Dione juno	70	Caligo telamonius
49	Dione moneta	71	<i>Caligo eurilochus</i>
50	Agraulis vanillae	72	Taygetis laches
51	Dryas iulia	73	<i>Magneuptychia libye</i>
52	<i>Eueides aliphera</i>	74	<i>Hermeuptychia hermes</i>
53	<i>Eueides isabella</i>		
54	Heliconius charithonia		
55	<i>Heliconius melpomene</i>		
56	Heliconius erato		