The effects of habitat type and disturbance on the species-richness of fruit-feeding butterflies at the Firestone Center for Restoration Ecology in Costa Rica

Emily Haber, Scripps College 2006

ABSTRACT

The fruit-feeding guild of nymphalid butterflies was sampled at the Firestone Center for Restoration Ecology (FCRE) in southwestern Costa Rica to investigate the effects of four habitat types on species-richness. Species-richness was expected to differ among riparian forest, secondary forest, bamboo forest and pastureland. Over two years and 53 sampling days, 1456 fruit-feeding nymphalid butterflies in 56 species and five subfamilies were caught at the FCRE. Observed species-richness was lowest in the riparian and highest in the secondary forest and pasture, but unequal samples were collected in each habitat. Rarefaction analysis showed that the pasture was the most species-rich and the bamboo the least species-rich. The observed species value in the riparian habitat fell along the rarefaction curve, indicating that the riparian zone may contain more species than indicated by raw data, although a species estimator predicted the riparian habitat to be the most species-poor. Species accumulation curves are still rising in each of the four habitats, indicating that additional fruit-feeding nymphalid species are present but have not yet been recorded. Greater species-richness in the most disturbed habitat suggests that highly disturbed habitats that are often overlooked may contribute greatly to the conservation of butterfly biodiversity.

INTRODUCTION

It is no surprise that anthropogenic disturbances put the world's tropical ecosystems at risk. These include logging, cattle farming, hunting, agriculture, housing and tourist development, and climactic change to name a few (Rosero-Bixby and Palloni 1998). Costa Rica is no exception. Although Costa Rica is a relatively small country, its tropical climate and geographical composition (ranging from sea level to 3800 m) provide more than fifteen distinct life zones that support extremely diverse flora and fauna (DeVries 1987). Despite a number of relatively well-established park reserves (23.4% of total land is protected), the amount of forest area remaining in 2000 was 39% of total land area (World Resources

Institute 2003)[1], and the Tropical Moist forest (5% remaining) and the Premontane Moist forest (2% remaining) are approaching elimination (Sánches-Azofeifa et al. 2001). Considering that Costa Rica's landscape is now highly fragmented, conducting both long-term spatial and temporal studies along with short-term rapid assessments of the rainforest flora and fauna is increasingly important for conservation purposes. Butterflies, which inhabit every continent save Antarctica, and occupy a wide range of terrestrial biomes including some extreme arctic tundra and high alpine habitats (Sbordoni and Forestiero 1984), have been targeted as a particularly useful indicator species. Butterflies are ubiquitous in the tropical forests of Costa Rica as well. This study explores the biodiversity of fruit-feeding nymphalid butterflies at a field station and reserve in southwest Costa Rica. More specifically, it investigates the comparative species-richness in four distinct habitats subjected to varying levels of anthropogenic disturbance: riparian, secondary forest, bamboo forest and pastureland.

Butterflies are taxomically well known and studied across a wide range of habitats and geographic regions; moreover, they are abundant and easily collected. These qualities, among others discussed later, make butterflies a desirable indicator group (Brown 1991). Indicator species are species that are closely tied to the health of their habitat (Noss 1990). They are particularly sensitive to changes in environment and habitat quality and can be used to serve as early warnings of ecosystem degradation or climactic change (Brown and Freitas 2000). Across the world there is a burgeoning wealth of information on tropical forest butterfly assemblages and the effects of land disturbance on these communities. A

---

[1] Total forest includes both natural forests and plantations, and is defined as land with tree crown cover of more than 10% of the ground and area of more than 0.5 hectares. The original forest as a percent of land area was 98%. Original forest is the estimated forest cover about 8,000 years ago assuming current climatic conditions (World Research Institute 2003).

considerable number of short-term studies have been conducted in the Neotropics (Shahabuddin and Terborgh 1999; Lewis 2001; Wood and Gillman 1998; Daily and Ehrlich 1995; Blau 1980). Although long-term studies are less common, continuing research was conducted on vertical stratification and the spatial and temporal dimensions of fruit-feeding butterflies in Ecuador (DeVries and Lande 1999; DeVries and Walla 2001, 1999; DeVries et al. 1997), and on the butterfly species of Costa Rica and their natural history (DeVries 1997, 1987). Brown has studied butterflies in the Brazilian Amazon and Atlantic Forests for over forty years and produced dozens of publications on the species-richness and community composition of butterflies, as well as the usefulness of insects as indicator species (Uehara-Prado et al. 2006; Brown and Freitas 2000; Brown 1991). Butterfly diversity, species-richness, and the effects of habitat disturbance were also studied (to name just a fraction of the extant examples) in Borneo (Hill et al. 2001; Hamer et al. 2003), in Indonesia (Hill et al. 1995; Veddeler et al. 2004) and in Vietnam (Spitzer et al. 1993), in the tropical rainforests of Australia (Hill and Jones 1992), and in several regions of Africa [West Africa: (Bossart et al. 2006; Ferman et al. 2003); Tanzania: (Fitzherbert et al. 2006); Madagascar: (Kremen 1994); Uganda: (Molleman et al. 2006)]. Most tropical insect communities are poorly characterized. Such an extensive accumulation of information on butterflies is extremely valuable because, when sampling at new locations such as the FCRE, immediate comparisons can be made with other sites and studies.

Along with being taxonomically and ecologically diversified, rapid reproduction, host plant reliance and sensitivity to environmental change make butterflies a useful indicator group (Brown 2000). Several studies in the past have shown that butterflies are both negatively (species-richness decreases) and positively (species-richness increases) indicative of habitat disturbance. Comparing species-richness in fruit-feeding butterflies (Nympalidae) in a successional gradient of secondary forest (old, intermediate and young) and mature forest in Indonesia, showed that mature forest and intermediate forest had a higher species-richness than young forest (Veddeler et al. 2005). Intermediate and old secondary forest did not differ, and the species-richness was related to the percent of shading in secondary forest (Veddeler et al. 2005). Further corroboration for the sensitivity of butterflies to environmental disturbance was presented by a study on selectively logged and unlogged forest in the lowland monsoon forests of Indonesia, which showed that species-richness, abundance, and evenness of butterflies were high in unlogged forest and there was a more complex butterfly community in unlogged forests (Hill et al. 1995). An experiment in the Atlantic Forest region testing the use of butterflies as indicators to measure changes in species diversity and community structure found that butterfly species-richness is well predicted by landscape connectivity and disturbance, and this suggests that select subfamilies can be used as rapid indicators of changes in the vegetational environment (Brown and Freitas 2000). In a more recent study evaluating the usefulness of fruit-feeding butterflies as indicators for forest disturbance, species-richness results showed that there was no effect of forest fragmentation, although there were distinctly different communities found in the fragmented versus continuous landscapes (Uehara-Prado et al. 2006).

Despite mounting evidence that butterflies are negatively affected by logging pressures and land fragmentation, there are also studies that have shown little negative, or even positive, effects of habitat disturbance on species-richness and abundance. Selective logging in a forest in Belize had little effect on the assemblage of fruit-feeding butterflies, and it is suggested that they are adapted to naturally disturbed habitats due to repeated hurricane damage and fires in this region (Lewis 2001). Application of the walk-and-count transect method (established by Pollard 1977) to determine how butterfly assemblages change between pairs of habitats differing in disturbance, showed that the most disturbed habitats in evergreen forest and semi-evergreen forest had the highest species-richness (21% and 110% more than undisturbed plots, respectively) and higher abundance (Wood and Gillman 1998). Butterfly assemblages across habitats and vertical space show marked temporal variation, both seasonally and annually (DeVries and Walla 2001, 1999; DeVries et al. 1997; Daily and Ehrlich 1995; Raguso 1990), and long-term studies are necessary to account for temporal changes and to render a more accurate estimate of species-richness (DeVries and Walla 2001).

In light of ongoing habitat degradation, this study documents the biodiversity of the fruit-feeding nymphalid butterflies at a field station and reserve of varying habitat disturbance in southwestern Costa Rica near the town of Dominical. Species accumulation was expected to show a predictable pattern of butterfly species-richness versus collecting effort that allows for analysis of the proportion of species recorded at FCRE thus far and for extrapolation. The total number of species in each habitat and species-richness was expected to differ in varying habitat types. This study presents baseline research in what is envisioned as a long-term, highly replicable butterfly study that will mark changes in fruit-feeding butterfly assemblages as reforestation efforts progress and the habitat and climate vary over time.

METHODS

There are two commonly accepted techniques for butterfly sampling: 1) walk-and-count transects, and 2) the sampling of fruit-feeding subfamilies of the butterfly family, Nymphalidae, using fruit-bait traps. This study used the latter technique to catch butterflies that feed on the juices of rotting fruits in cylindrical banana-baited traps. The fruit-feeding guild is composed of species that derive adult nutritional requirements almost completely from rotting fruit juices (commonly referred to as fruit-feeding nymphalids). Fruit-feeding nymphalid butterflies comprise an estimated 40% to 55% of the total nymphalid species present in tropical forests (DeVries 1999), and include species belonging to the following subfamilies: Charaxinae, Morphinae, Brassolinae, Amathusiinae, Satyrinae, Nymphalinae (some genera) (DeVries and Walla 2001). Sampling using the fruit-baited traps is a preferred method because it is standardized and can be replicated across a wide range of habitats and geographic regions, and reduces human error resulting from sight identification in walk-and-count transects or hand-netting methods. In addition, fruit-feeding nymphalids are mostly confined to tropical forests and are one of the most well-understood butterfly families taxonomically (DeVries 1997).

Conservationists interested in rapid sampling have suggested the use of extrapolation techniques for estimating the total number of butterfly species in a given area by extrapolating from a targeted indicator taxa (Kremen 1994, Beccaloni and Gatson 1994; Brown and Freitas 2000). Beccaloni and Gatson looked at pre-collected butterfly data from 21 sites and found that across all sites the average proportion of Ithomiinae is 4.6% of the total species present, and conclude that since there is relatively low variance in this percentage, it is possible to predict the overall species-richness if the number of Ithomiinae at a site is known. Although Ithomiinae is a Nymphalidae subfamily, species are seldom found feeding on fruit; therefore, this particular subfamily would not be useful as an indicator species in this study. Another more directly pertinent study in the Amazon showed that

Nymphalidae, which made up 25% to 29% of the total butterfly community, was best correlated with the entire butterfly fauna (Brown and Feitas 2000). Total butterfly species richness was predicted to be *ca* 3.7 ± 0.23 times the total Nymphalidae species found, and this number may be applicable to other butterfly communities in the Neotropics (Brown and Freitas 2000). Although a comprehensive checklist of a butterfly community is best derived by a composite of hand netting, visual identification, and baited traps, fruit-baited traps alone are fitting for replicable long-term studies and research that looks at vertical dimensions. Additionally, it is possible that with further research, extrapolation techniques can be used to gain a rough estimate of total species-richness from a well-recorded nymphalid community.

Study Site

Fieldwork took place at the Firestone Center for Restoration Ecology (FCRE) located on the southwest coast of Costa Rica (9.279 N; 83.862 W). The 60-hectare reserve and field station was originally lowland moist rainforest before it was cleared for cattle farming in the 1950s and 1960s. Only a few patches of forest in riparian areas remained before restoration and sustainable forestry efforts began in the early 1990s. In 2005, proprietorship was transferred to Pitzer College, and the property is now a biological field station for undergraduate research and education. The FCRE is presently covered primarily by secondary tropical moist forest and non-native bamboo forest, and also contains smaller patches of pasture land and a few relatively pristine riparian zones. Through Pitzer College's stewardship, the long-term goal is to restore the land over the next four decades to primary rainforest, and to monitor changes in the center's floral and faunal biodiversity.

Trap Construction

Trap construction was modeled after the Tropical Ecology, Assessment, and Monitoring (TEAM) Initiative butterfly monitoring protocol produced by the Center for Applied Biodiversity Science at Conservation International. Slight alterations were made in the design (see Appendix 1 for trap dimensions and photographs).

Each trap consisted of a cloth cylinder made of mosquito netting with a metal ring frame at the top and bottom. A collar was sewn to the top and the bottom of the mosquito netting to attach the support rings to the netting. The top of the trap was closed-off with mosquito netting while the bottom was left open as the point of entry. Trapped butterflies were accessed through a 25 cm slit down the middle of the cylinder. A nonflexible plastic plate was attached to the bottom ring of the trap and a red bait bowl was bolted to the center of the plastic with its lip slightly above the bottom cylindrical ring. Butterflies feeding on the bait entered through the bottom and flew up upon attempted exit, resulting in entrapment at the upper portion of the trap. Each trap was filled with a mixture of rotting banana, beer, and honey. Bait was replaced simultaneously in all traps twice per week, or more frequently if needed.

Trap Placement

Traps were placed in four distinct habitat types: secondary forest, bamboo, pasture, and riparian forest. Three pairs of traps were placed in the secondary zone, the bamboo zone, and the riparian zone (total=six traps per zone). Pairs of traps were stratified so that one trap was in the understorey (mean height 0.84 m) while the other trap was placed directly above it in the upper story of vegetation (mean height 6.51 m). Traps were hung from nylon ropes running over tree branches so that the traps could be lowered and raised from the ground daily to release individuals and to refill bait cups. In the pasture, three separate lower-level traps were hung from trees amidst tall grass. Traps were not stratified because pasture trees were not tall enough to support upper-level traps. Trees, grasses, and shrubs in the pasture showed remarkable growth over the span of one year and trees in the pasture will be tall enough to stratify traps in the near future.

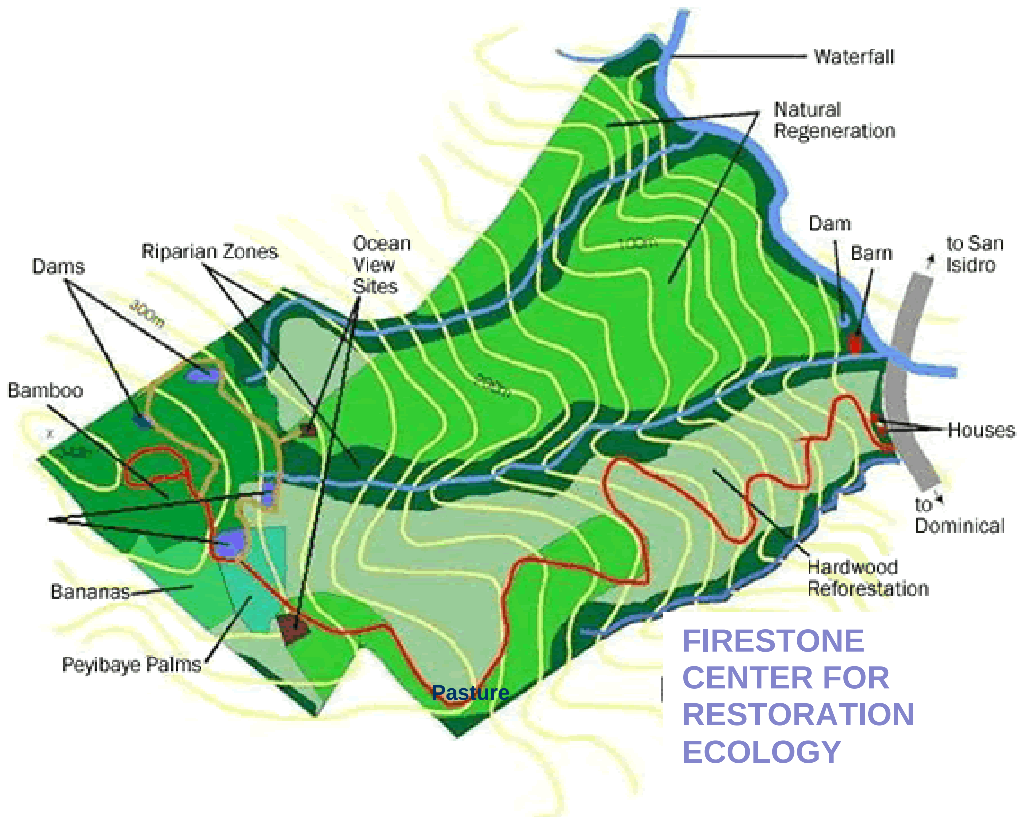

Figure 1. Map of the Firestone Center for Restoration Ecology

Procedure

Fieldwork was conducted from 1 June to 26 June in 2005 and from 15 June to 25 July in 2006, for a total of 53 sampling days. Each trap was checked and emptied once per day in the late afternoon. The species present and their abundances were recorded before release. Butterflies were not marked, so some individuals may have been recaptured. Species that were not identified in the field were collected and taken back to the field station for identification (using DeVries 1987) and mounted (See Appendix 2 for species list and photographs).

Statistical Analysis

Species accumulation curves were plotted for each habitat type to assess the rate of species accumulation in each habitat and to determine if curves had reached an asymptote demarking species saturation. To account for an unequal number of individuals caught in each habitat, the cumulative number of individuals collected was plotted against the cumulative number of species in the order of collection.

Rarefaction methods (Sanders 1968; Hulbert 1971; Simberloff 1972) are used to compare species richness among areas of differing sampling effort. Brzustowks (2006) defines rarefaction as a method that takes hypothetical subsamples of n ($n <$ total sample size) individuals from the most-sampled region, and calculates the expected number of species in these subsamples. The rarefied sample can then be compared to observed species values from less sampled areas. A rarefaction curve was calculated with 95% confidence intervals to test if the butterfly species-richness was significantly different among habitats. The rarefaction curve was calculated using an online rarefaction calculator (Brzustowski 2006) and used the most-sampled region, the secondary forest habitat, to calculate the average number of species that would be found in this habitat in smaller subsamples. The values composing this curve are compared to the actual number of species found in each habitat and the standard deviation is used to analyze statistical significance. The total species-richness of fruit-feeding nymphalid butterflies in each habitat and the entire reserve was estimated using Chao1 richness estimator in the program EstimateS v.7.5 (Colwell 2006).

RESULTS

A total of 1456 fruit-feeding nymphalid butterflies in 56 species and five subfamilies were caught at the FCRE. Additionally, three Hesperioidea (skipper) species were found in the fruit-baited traps. Over 55% of the species were represented by three or fewer individuals, and 63%, 52%, 66%, and 22% of total species were found in the secondary, bamboo, pasture and riparian, respectively. Species accumulation rates were relatively equal in the bamboo and secondary habitats, and comparable to the accumulation rate of the entire property (Fig. 2). Species accumulation occurred more rapidly in the pasture habitat. The total property curve is nearly asymptototic while the other four habitats are still rising relatively steeply, indicating that more sampling is necessary to determine total species-richness in each habitat. In 2005 there were significantly more butterflies found in the lower secondary traps than found in the lower bamboo, lower pasture, and lower riparian traps (Haber 2005). This was not the case, however, in 2006 (Haber 2006) (Fig. 3). The differences between 2005 and 2006 may indicate a potentially substantial effect of temporal variation in the abundance of butterflies and, consequently, the number of species in each habitat.

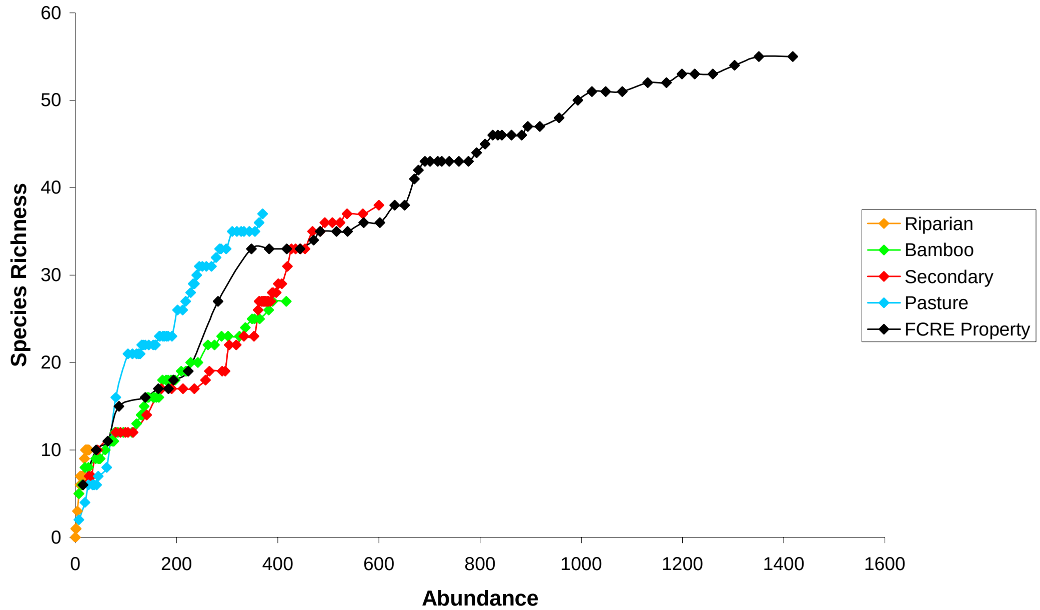

Figure 2. Species accumulation curves showing cumulative species versus cumulative individual abundance through time in four habitats and the entire FCRE property.

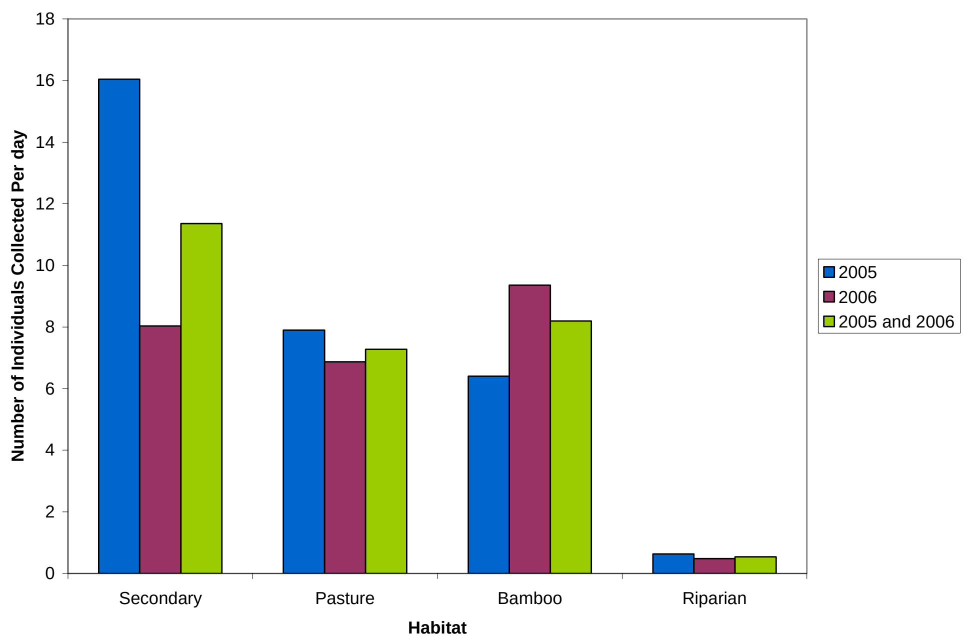

Figure 3. Comparison of the number of individuals found in each habitat per day in 2005, 2006, and 2005 and 2006 combined.

Over the duration of the study the observed number of species was greater in the secondary forest and the pasture, but numbers of individuals sampled in each habitat differed and rarefaction analysis corrected for the uneven sampling of butterflies among habitats. Rarefaction of the secondary forest sample indicates, in contrast to the raw results uncorrected for sample size, that the riparian and secondary forest habitats are expected to contain a similar number of species, while the bamboo forest fell below and the pasture was above the curve and its 95% confidence intervals (Fig. 4). The bamboo habitat was 2.58 standard deviations less than the rarefaction curve value for the same subsample size in the secondary forest and the bamboo was 2.25 standard deviations more than would be expected. This suggests that should sampling continue in all habitats until the species accumulation reached satiation, that the pasture would have the greatest number of individuals while the secondary forest and riparian habitats would have similar species-richness and the bamboo would contain the least species.

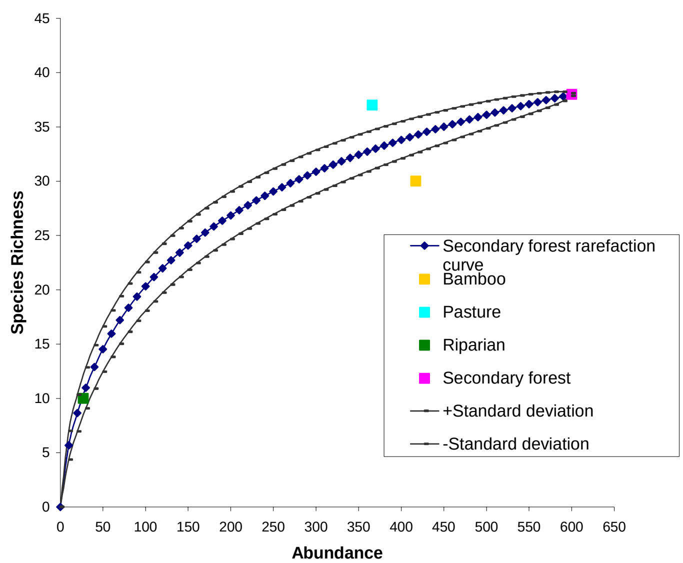

Figure 4. Rarefaction curve and 95% confidence interval for the sample of fruit-feeding nymphalids in the secondary forest compared to number of observed species in each habitat.

True species estimates using the Chao1 species estimator predicted more species in the pasture and bamboo habitats (54 and 52 mean value, respectively) than in the secondary (44) and riparian habitats (13). However, 95% confidence intervals for the species estimation in the pasture, bamboo, and secondary forest strongly overlap, making comparisons of the species estimation for these three habitats insignificant. The number of species in the riparian habitat is estimated to be significantly lower than the pasture, secondary, and bamboo habitats, and the 95% confidence intervals do not overlap with the species estimates for the other three habitats (Fig. 5).

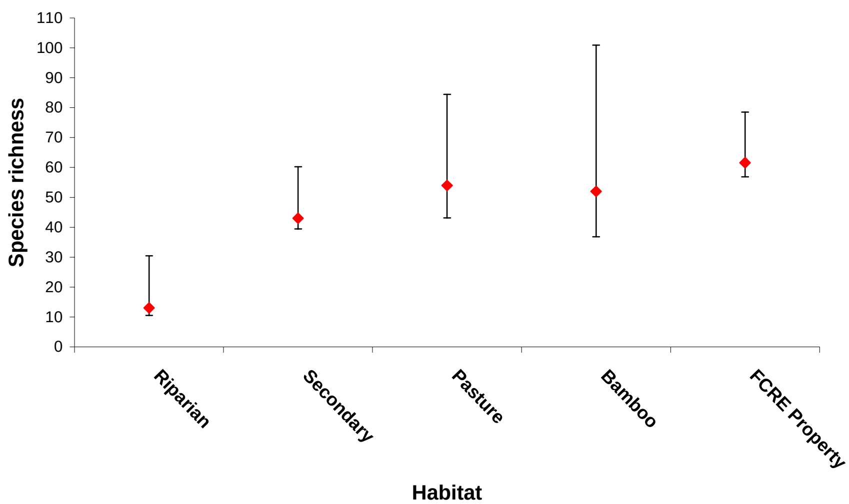

Figure 5. Estimate of mean number of species and 95% confidence intervals for each habitat and the entire reserve.

DISCUSSION

Data collection

Sampling with fruit-baited traps proved to be an effective and highly repeatable method for sampling fruit-feeding nymphalids. Results, however, should be interpreted with some caution considering that species accumulation curves have not asymptoted in each habitat or on the property. Additionally, only three trap pairs were placed in each habitat type (three single traps in the pasture) at one location in the specified habitat type. To strengthen the effectiveness of sampling as well as the reliability of the results, more traps should be placed across the entire area of the property. Butterflies were only sampled for a portion of the wet season, and species diversity and community composition in the tropics show significant temporal variation, peaking in the rainy season and declining in the dry season and showing significant monthly variation as well (DeVries and Lande 1999).

Cautionary notes aside, this study unveiled some novel results on butterfly species-richness in the face of habitat disturbance and underscored the surprisingly depauperate state of the less disturbed riparian habitat (this portion of the property was not deforested). Although there are several studies signifying that habitat disturbance leads to a decrease in species diversity (i.e. 2005 Veddeler et al.; Hill et al. 1995), there is no clear consensus on the effects of anthropogenic disturbance of tropical forests on butterfly communities. This study showed that although overall butterfly abundance was greater in the less disturbed secondary forest, the pasture accumulated species more efficiently (more species found in a smaller number of individuals caught) than the secondary and bamboo forest. Rarefaction analysis showed that the pasture had the greatest species-richness. Although counterintuitive, other studies have shown that habitat disturbance can be positively correlated with butterfly abundance and richness. Spitzer et al. (1993) found that highly disturbed ruderal habitats (cultivated and abandoned land) had higher species diversity and abundance than closed forest. Species found most often in the disturbed habitats also had a greater geographic range, were most widely distributed, and had higher population sizes (Spitzer et al. 1993). Walk-and-see transects in a study in Trinidad also showed that the most disturbed habitats were the most species-rich (Wood and Gillman 1998). In contrast, DeVries et al. (1997) found that an edge region where primary forest interfaced pasture had significantly lower species-richness than primary, higraded (selectively logged), and secondary forest. Intermediately, studies have also shown that selective logging has neither positive nor negative effects on species-richness and diversity (Hamer et al. 2003; Lewis 2001), although this does not necessarily offer information in changes in the composition of species living in logged versus unlogged environments.

The pastureland at the FCRE is no longer cattle grazed and has remained free from anthropogenic disturbance since 2005. This land has demonstrated marked regrowth, and although a highly unnatural environment, grasses, shrubs, small trees, and other flora contained within may provide important host plant resources. The pastureland is situated adjacent to secondary and bamboo forest, making it possible that some individuals were drawn from surrounding areas, given that species associated with disturbed habitats may have a greater range (Spitzer et al. 1993). There are certainly some highly abundant species shared between the pasture, secondary, and bamboo forest habitats (Appendix 3). Capture/recapture data shows that traps can draw in individuals previously trapped 50-400 meters away, although recapture rates from distances this great were relatively infrequent (Hill et al. 2001).

The riparian habitat, in which only 27 individuals and 10 species were captured over 50 sampling days, showed the lowest observed species-richness as well as a significantly lower estimated species-richness value when compared to the other three habitats. The observed species in the selected riparian habitat, however, fell almost exactly on the rarefaction curve, indicating that equally low subsamples of the secondary forest have similar species-richness. This result mirrors the results of a study on fruit-feeding nymphalids in the Ecuadorian rainforest. Based on observed species-richness, the primary forest had the lowest species-richness and the fewest unique species, but rarefaction analysis showed that the observed value fell within the 95% confidence intervals of the curve, indicating that the primary forest is perhaps more diverse than shown by raw data (DeVries et al. 1997). The question then becomes, would the riparian zone prove to be as species rich as other habitats given the right amount of sampling, or are butterflies simply not present in the riparian habitat? Only further sampling can answer this question.

Light levels have an enormous effect on species-richness and abundance (Hamer et al. 2003; Sparrow et al. 1994). Sampling along a road transect following a wide, continuous light gap produced 74% more butterfly species than a trail transect that went through scattered light gaps in a forest, and large natural light gaps are likely to attract a great number of species in undisturbed primary forest as well (Sparrow et al. 1994). Riparian traps were placed in a zone with thicker canopy cover, and low abundance in the riparian zone was probably correlated with low light levels. Butterflies were attracted more frequently to fruit-bait traps placed along rivers in more illuminated zones within the forest and along developed riparian areas (personal observation).

The non-native bamboo forests (Species: *Guadua augustifolia* and *Dendrocalamus asper*) attracted fewer individuals than would be expected according to rarefaction, but nonetheless contained the second greatest number of individuals (following secondary forest) and 30 species. Species-richness may be lower in the bamboo because it is a non-native and homogeneous habitat. It has, however, become an important habitat for many species at the

FCRE. Many Morphinae, Brassolinae, Satyrinae, and Hesperiinae are dependent upon bamboo patch resources (Brown and Freitas 2000), and there may be a decline in species-richness at the FCRE if bamboo is removed to restore the property to a more natural state.

CONCLUSION

When deciding what type of land is appropriate to conserve in an attempt to maximize butterfly species diversity, short-term and long-term field research is imperative. Fruit-feeding nymphalid butterflies are found widely throughout the tropics and fruit-bait sampling provides a standardized method ripe for comparison among years and geographic regions. This study indicates that secondary forest, bamboo forest, and pasture are important habitats to conserve for maximizing butterfly biodiversity. Finding that species-richness corrected for sample size is greatest in the most highly and recently disturbed habitat underscores the importance of conserving disturbed habitats that are often marginalized for conservation purposes. Although the most mature and undisturbed habitat (the riparian forest) was estimated to be the least species rich and had extremely low individual abundance, this does not mean that primary forest is not important in butterfly conservation. Primary forest is essential for shade preferring species and often supports endemic species. While species that live in disturbed habitats can travel over a wider geographic range, species that are found in closed canopy forest are often restricted to that habitat (Spitzer et al. 1993), making conservation of intact forest particularly important. Disturbed and selectively logged land, however, can also contribute significantly to butterfly conservation efforts. Given the varying results in the effects of habitat disturbance on tropical butterfly assemblages, research and environmental policies targeting maximal butterfly biodiversity should certainly point toward conserving primary and secondary forest, but should consider conserving the sometimes marginalized disturbed habitats as well.

AKNOWLEDGMENTS

This Project was funded by a grant from the Mellon Foundation to the Joint Science Department, Scripps College in 2005 and 2006. Many thanks to Dr. Donald McFarlane for guidance and support throughout this study. Thanks to Dr. Diane Thomson for reviewing and advising. Thank you to Keith Christenson for guidance in mapping and assistance on the experimental setup. Thanks to FCRE summer research students, Elspeth Llewellyn, Christopher Wheeler, Jenny Aleman-Zometa, Kelly Janes, Callae Snively, and LuAnna Dobson for field research assistance. Thank you to Nancy Haber for assistance in trap construction.

REFERENCES

Beccaloni, G.W. and Gatson, K.J. 1994. Predicting the Species-richness of Neotropical Forest Butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. Biological Conservation 71: 77-86.

Blau, W.S. 1980. The Effect of Environmental Disturbance on a Tropical Butterfly Population. Ecological Society of America 61: 1005-1012.

Bossart, J.L, Opuni-Frimpong, E., Kuudaar, S. and Nkrumah, E. 2006. Richness, abundance, and complementarity of fruit-feeding butterfly species in relict sacred forests and forest reserves of Ghana. Biodiversity and Conservation 15: 333-359.

Brown, K.S. Jr., 1991. Conservation of neotropical environments: insects as indicators. In: Collins N.M., Thomas J.A., eds. *The conservation of insects and their habitats.* London: Academic Press, 449-504.

Brown, K.S. Jr and Freitas, A.V.L. 2000. Atlantic Forest Butterflies: Indicators for Landscape Conservation. Biotropica 32: 934-956.

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

DeVries P.J. 1987. *The Butterflies of Costa Rica and their Natural History. I:Papilionidae, Pieridae and Nymphalidae.* Princeton, NJ: Princeton University Press.

DeVries PJ. 1997. *The Butterflies of Costa Rica and their Natural History. II: Riodinidae.* Princeton, NJ: Princeton University Press.

Devries, P.J. and Lande, R. 1999. Associations of co-mimetic Ithomiine butterflies on small spatial and temporal scales in a neotropical rainforest. Biological Journal of the Linnean Society 67:73-85.

DeVries, P.J., Murray, D. and Lande, R. 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.

DeVries, P.J. and Walla, T.R. 1999. Species diversity in spatial and temporal dimesnsions of fruit-feeding butterflies from two Ecuadorian Rainforests. Biological Journal of the Linnean Society. 68: 333-353.

DeVries, P.J. and Walla T.R. 2001. Species diversity and community structure in neotropical fruit-feeding butterflies. Biological Journal of the Linnean Society 74: 1-15.

Fermon, H., Walter, M. and Muhlenberg, M. 2003. Movement and vertical stratification of fruit-feeding butterflies in a managed West African rainforest. Journal of Insect Conservation 7: 7-19.

Fitzherber, E., Toby, G., Davenport, T.R.B., and Caro, T. 2006. Butterfly species-richness and abundance in the Katavi ecosystem of western Tanzania. African Journal of Ecology 44: 353-362.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryatis, M. and Chey, V.K. 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. Journal of Applied Ecology 40: 150-162.

Hill, J.K., Hamer, K.C., Tangah, J. and Dawood, M. 2001. Ecology of tropical butterflies in rainforest gaps. Oecologia 128: 294-302.

Hill, J.K., Hamer, K.C. Lace, L.A. and Banham. 1995. W.M.T. Effects of Selective Logging on Tropical Forest Butterflies on Baru, Indonesia. The Journal of Applied Ecology 32: 754-760.

Hill, C., Gillison, A., and Jones, R. 1992. The Spatial Distribution of Rain Forest Butterflies at Three Sites in North Queensland, Australia. Journal of Tropical Ecology 8: 37-46.

Hurlbert, S.H. 1971. The non-concept of species diversity: a critique and alternative parameters. Ecology 52:577-586.

Kremen, C. 1994. Biological Inventory Using Target Taxa: A Case Study of the Butterflies of Madagascar. Ecological Applications 4: 407-422.

Lewis, O.T. 2001. Effect of Experimental Selective Logging on Tropical Butterflies. Conservation Biology 5: 389-400.

Molleman, F., Kop, A., Brakefield, P.M. DeVries, P.J. and Zwaan, B.J. 2006. Vertical and temporal patterns of biodiversity of fruit-feeding butterflies in a tropical forest in Uganda. Biodiversity and Conservation 15: 107-121.

Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. Biological Conservation 12: 115-134.

Raguso, R.A. 1990. The butterflies (Lepidoptera) of the Tuxtlas Mts., Veracruz, Mexico, revisited: Species-richness and habitat disturbance. Journal of Research on the Lepidoptera 29: 105-133.

Rosero-Bixby, L. and Palloni, A. 1998. Population and Environment: A journal of Interdisciplinary Studies 20 (2). Human Sciences Press, Inc.

Sánches-Azofeifa, G.A., Harriss, R.C. and Skole, D.L. 2001. Deforestation in Costa Rica: A quantitative analysis using remote sensing imagery. Biotropica 33: 378-384.

Sbordoni V. and Forestiero S. 1984. *Butterflies of the World*. Willowdale, Ontario, Cananda: Firefly Books (U.S.) Inc.

Sanders, H.L. 1968. Marine Benthic Diversity: A Comparative Study. The American Naturalist 102: 243-282.
Shahabuddin, G. and Terborgh, J.W. 1999. Frugivorous butterflis in Venezuelan forest fragments: abundance, diversity and the effects of isolation. Journal of Tropical Ecology 15: 703-722.
Simberloff, D. S. 1972. Properties of the rarefaction diversity measurement. American Naturalist 106: 414-418.
Sparrow, H.R., Sisk, T.D., Ehrlich, P.R., Murphy, D.D. 1994. Techniques for Monitoring Neotropical Butterflies. Conservation Biology 8: 800-809.
Spitzer, K., Novotny, V., Tonner, M. and Leps, J. 1993. Habitat preferences, distribution and seasonality of the butterflies (Lepioptera, Papilionoidea) in a montane tropical rain forest, Vietnam. Journal of Biogeography 20: 109-121.
Uehara-Prado, M. Brown, K.S. Jr. and Freitas, A.V.L. 2006. Species-richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. Global Ecology and Biogeography, Journal compilation Blackwell Publishing Ltd.
Veddeler, D., Schulze, C.H., Steffan-Dewenter, I., Buchori, D. and Tscharntke, T. 2005. The contribution of secondary forest fragments on the conservation of fruit-feeding butterflies: effects of isolation and age. Biodiversity and Conseveration 14: 3577-3592.
Wood, B. and Gillman, M.P. 1998. The effects of disturbance on forest butterflies using two methods of sampling in Trinidad. Biology and Conservation 7: 596-616.

WEB BASED CITATIONS

Brzustowski, John. 2006. http://www2.biology.ualberta.ca/jbrzusto/rarefact.php. Rarefaction Calculator. November 20, 2006.
Batra, Puja. Tropical Ecology, Assessment Butterfly Monitoring Protocol. The Center for Applied Biodiversity Science ant Conservation International. 19 November 2006. http://www.teaminitiative.org/portal/server.pt?open=512&objID=396&mode=2&in_hi_userid=124626&cached=true.
Colwell, R.K. and Coddington, J.A. 2006. EstimateS: Statistical Estimation of Species-richness and Shared Species from Samples. Version 7.5 User’s Guide and application published at http://viceroy.eeb.uconn.edu/estimates.
Haber, E. 2005. http://costarica.jsd.claremont.edu/library.shtml. Baseline assessment of butterfly biodiversity and community composition.
Haber, E. 2006. http://costarica.jsd.claremont.edu/library.shtml. Continued baseline assessment of butterfly biodiversity.
World Research Institute. Earthtrends 2003. Country Profiles. Forest, Grasslands, and Drylands—Costa Rica. http://earthtrends.wri.org/pdf_library/country_profiles/for_cou_188.pdf