

Occurrences of forest butterflies in the farm bush savannah outside a forest reserve in Ghana, West Africa

Jean P. Elbers^{1*} and J.L. Bossart²

¹Department of Biology, Missouri State University, Springfield, Missouri 65897, USA; ²Department of Biological Sciences, Southeastern Louisiana University, Hammond, Louisiana 70402, USA

(Accepted 17 August 2009)

Abstract. The willingness of a species to leave a forest fragment is a prerequisite for subsequent dispersal across the intervening non-forested landscape. Species with stringent fidelity to the forest patch will be isolated from populations in other fragments and predisposed to factors that promote extinction of local populations. Here, we document which fruit-feeding, forest-dwelling butterflies occur in the farm bush savannah outside an afrotropical forest reserve in order to gain a first approximation of those potentially dispersing across it. Standard fruit-baited traps hung at 80 m inside the forest, the forest edge and 12 and 50 m into the savannah matrix were used to characterize communities in the different habitats. A total of 1616 specimens were collected from the 19 traps, representing 90 species. Rarefied species richness was generally comparable across habitats. Multivariate ordination analyses, which integrate species composition and relative abundance in addition to richness, uncovered two broad community types, i.e. forest (edge plus 80 m inside) and matrix. Relative fidelity to forest habitat was investigated for the 45 species that were represented by at least five individuals. More than half of the forest-associated species showed relaxed fidelity to forest habitat and were commonly trapped in the matrix. Although forest generalists and dry forest species were expected to be more commonly trapped outside the forest relative to wet or moist forest species, there was no relationship between the relative occurrence of species in matrix *versus* forest habitat and their habitat association category.

Key words: Afrotropics, forest fragments, fruit-feeding butterflies, habitat fidelity, matrix habitat, Nymphalidae, patchy landscapes

Introduction

Ghana, West Africa, has among the highest rates of forest destruction in the world (Hall and Swain, 1981), mostly due to the clearing of forests for agriculture and from logging for timber. Only approximately 13% of original forest cover remains (Sayer *et al.*, 1992; Poorter *et al.*, 2004; although see Fairhead and Leach, 2002). This human transformation of what was originally an expansive and

largely contiguous forested landscape has resulted in relatively small, isolated patches of remnant forest surrounded by anthropogenically derived farm bush savannah (Hall and Swain, 1981).

Species populations in remnant forest patches are potentially isolated from other populations if individuals are unable or unwilling to disperse across the surrounding non-forest landscape matrix. Isolation of populations reduces effective population size and causes loss of genetic diversity due to genetic drift and inbreeding depression (Young *et al.*, 1996). Genetic diversity is essential for

*E-mail: elbers1@missouristate.edu

adaptive change, and its loss decreases evolutionary flexibility and can ultimately lead to species extinctions (Lande, 1988; Primack, 2004). Connectivity of patchy populations via dispersal of individuals and subsequent genetic exchange, or gene flow, serves to maintain genetic diversity and to counter factors that promote extinction of local populations. In Ghana, no substantial intact forest habitat exists outside gazetted reserves, but the shreds of riparian forests, overgrown cocoa groves and plantations, and numerous sacred forest groves scattered throughout the matrix may serve as dispersal stepping stones that help to connect spatially separated forest communities, particularly for species that experience farm bush savannah as relatively benign.

Determining which forest-associated species are resistant to the isolating effects of fragmentation due to dispersal among habitat patches is a formidable challenge. Mark-release-recapture studies are logistically prohibitive when fragments are separated by significant distance, and interpretation of dispersal estimates derived from genetic analyses is not straightforward (Bossart and Pashley-Powell, 1998). Certainly though, lack of fidelity to the forest patch is a prerequisite for dispersal across landscapes. Species vary in their dependency on patch resources and their tolerance of habitat degradation and environmental conditions outside the forest. This variability is manifested as species-specific differences in willingness and ability to venture out of and away from a forest patch (Gascon *et al.*, 1999; Ricketts, 2001; Horner-Devine *et al.*, 2003; Vandergast and Gillespie, 2004). Species with stringent specificities to the particular environmental conditions of forests, even those that are relatively strong dispersers, will be less likely to occur in the surrounding non-forest matrix than species having more flexible tolerances (Klein, 1989; Bender *et al.*, 1998; Villard, 1998; Kotze and Samways, 1999; Rosenblatt *et al.*, 1999). Documentation of which forest species occur in the matrix thus gives a first approximation of those potentially dispersing across it.

Here, we quantify the community of fruit-feeding butterflies at the forest edge and in the farm bush savannah outside a forest reserve in Ghana. Out of the approximately 900 butterfly species known for Ghana, nearly 80% are centred on forest habitat and approximately one-third of these forest species are fruit feeders as adults (Larsen *et al.*, 2007). The occurrence and distribution of fruit-feeding butterflies within forest fragments in Ghana have been investigated (Bossart *et al.*, 2005, 2006; Larsen *et al.* 2007; Bossart and Opuni-Frimpong, 2009). However, virtually no systematic empirical data have been collected on which of these forest butterfly species are found in the non-forest matrix.

Materials and methods

Study location

The study was conducted at Bobiri Forest Reserve (hereafter, Bobiri forest), which is located in the moist semi-deciduous forest zone southeast of Kumasi, Ghana (6°41'N, 1°21'W). Bobiri forest is a managed reserve that covers approximately 5000 ha. Bobiri forest is also approximately 16 km distant from the next closest forest fragment, the 8 ha Bonwire sacred grove, and approximately 40 km distant from the next substantial expanse of forest, the 1200 ha Owabi Wildlife Sanctuary. Logging in Bobiri forest is regulated by the Ghana Forestry Commission and is prohibited within the area designated as the Bobiri Butterfly Sanctuary, an ecotourism site located within the southwestern portion of the forest.

Trap samples

We used standard fruit-baited traps to survey the fruit-feeding butterflies occurring in the savannah matrix bounding the southwest perimeter of Bobiri forest, which includes the Bobiri Butterfly Sanctuary. Five 50 m forest edge to savannah transects were established along an approximately 2 km section of forest. Transects were set by walking perpendicular from the forest edge into the savannah matrix using a compass to set direction and a metre tape to determine distance. Traps were hung approximately 10 cm from the ground at the forest-savannah edge and at 12 and 50 m distant from the edge for a total of 15 traps (three per transect). The two matrix distances were incorporated to test whether species differed in the extent to which they would move into the matrix. Edge traps were hung on understory trees; matrix traps were hung on steel rebar rods bent at a 90° angle and driven into the soil. For ease of reference and discussion, trap locations will hereafter be referred to as Elbers-edge (E-edge), near matrix and far matrix habitats, respectively. Transects were established in areas having similar forest canopy cover and matrix habitat and separated from each other by at least 400 m. Sampling occurred between 13 June and 12 July 2007, and included 14 total sampling bouts. Each sampling bout consisted of baiting traps with a mixture of fermenting banana and palm wine and retrieving collections approximately 24 h later.

To increase the interpretive context of the current study, these data were compared with forest trap data collected by Bossart from the same area of Bobiri forest between 2005 and 2006. In this earlier study, paired traps were hung approximately 15 cm above the forest floor at the forest edge (hereafter

Bossart-edge (B-edge)) and 80 m from the edge in the forest interior (hereafter Bossart-forest (B-forest)). Trap pairs were established at two locations separated by nearly 2 km for a total of four traps and were sampled approximately every 3 weeks for a total of 14 sampling bouts. Comprehensive analysis and discussion of the fruit-feeding butterfly community within Bobiri forest have been published elsewhere (Bossart *et al.*, 2005, 2006; Bossart and Opuni-Frimpong, 2009).

Collected specimens were identified using Larsen (2005). The vast majority of Ghana's butterflies can easily be identified based on wing colour patterns and wing morphology. The few difficult specimens were identified with assistance from Dr John Rawlins, Associate Curator, Section of Invertebrate Zoology, Carnegie Museum of Natural History, USA.

Data analysis

Community diversity of each habitat, i.e. edge, forest, and near and far matrix, was analysed utilizing both univariate (rarefied species accumulation curves and Simpson's index of diversity) and multivariate (non-metric multidimensional scaling ordination (NMDS)) methods. Rarefaction curves and 95% confidence intervals were constructed to standardize sample size across habitats being compared and were generated using EcoSim 7.00 (Gotelli and Entsminger, 2003). Simpson's index, which gives the most robust measure of overall community heterogeneity (Magurran, 2003), was computed using EstimateS 7.5 (Colwell, 2005). Trap data for each habitat were pooled across sampling bouts prior to analysis.

NMDS, which is considered the best ordination analysis for multivariate data (McCune and Grace, 2002), reduces lists of species and their abundances into a single measure of dissimilarity between all pairs of samples. An iterative procedure then optimizes the arrangement of samples in multi-dimensional space such that rank order among sample dissimilarity is preserved in the rank order of spatial distances. The NMDS analysis was conducted using CAP 3.11 (Pisces Conservation

Ltd, 2005). Raw data were square root transformed prior to calculation of the initial Bray–Curtis dissimilarity matrix. The program was run for 200 iterations using a randomly calculated initial starting point.

To quantify the relative fidelity of forest species to forest habitat, we calculated the percentage occurrence of each species in each habitat. We restricted the analysis to those species represented by at least five individuals in order to have confidence in percentages obtained (Appendix 1). Habitat occurrence data were then compared with Larsen *et al.*'s (2007) independently determined habitat association categories, which were compiled over a decade of collecting in preparation for the book, *The Butterflies of West Africa* (Larsen, 2005). Species are characterized as wet forest (WEF), moist forest (MEF), dry forest (DRF), all forests (ALF), Guinea savannah (GUI), Sudan savannah (SUD) or ubiquitous (UBQ) species, based on their distribution and abundance in these habitats. We predicted that the forest species with the lowest fidelity to Bobiri's moist forest habitat and therefore most likely to occur in the savannah matrix would be those associated with dry forests or all forest types, given their presumed higher tolerance of drier, more open environments. We conversely expected those species with the highest fidelity to moist forest habitat and least likely to occur in the matrix would be those known to be centred on moist or wet forest subtypes.

Results

Community diversity analysis

A total of 1616 individuals was collected from the 19 traps, representing 90 species (Appendix 1). The number of species trapped from each habitat area ranged from a low of 33 at B-forest to a high of 52 at E-edge (Table 1). However, species accumulation curves were still rising in all cases, indicating that species saturation had not been reached and more species would have been collected had sampling continued (Fig. 1). Only the B-forest sample showed a rate of accumulation that seemed to be slowing.

Table 1. Summary trap collection data

Habitat	Total individuals	Individuals per trap (mean \pm SE)	Observed species richness	Simpson's diversity
B-forest	140	70 \pm 0	33	17.3
B-edge	153	77 \pm 25	39	14.02
E-edge	448	90 \pm 25	52	15.52
Near matrix	433	87 \pm 11	47	9.53
Far matrix	442	88 \pm 4	46	7.13

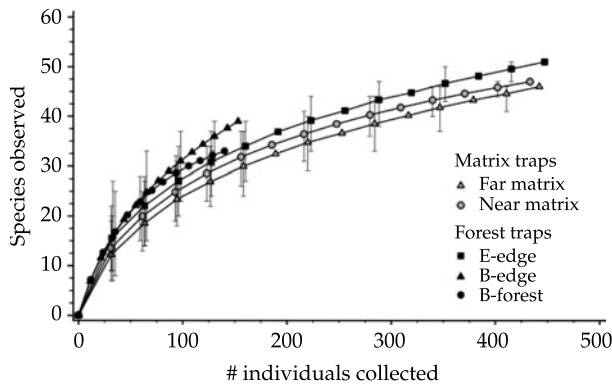


Fig. 1. Individual-based rarefied species accumulation curves for fruit-feeding butterflies in four surveyed habitats.

Rarefied species richness, which controls for sample size differences, was comparable across habitats at nearly all sub-sample sizes. The total 40 species collected from B-edge, however, exceeded the rarefied estimates and their 95% confidence intervals for the other four habitats. Also, significantly more species were collected from E-edge at the largest sub-sample size relative to the number collected from either of the matrix habitat sites (Fig. 1). Simpson's index of diversity, which integrates both the number of species and their relative abundances, was lower by 40% or more for samples collected from the matrix traps relative to those collected from edge or forest traps (Table 1).

Ordination analysis

The NMDS analysis produced two distinct groups (Fig. 2). The first group consisted of all the matrix trap collections, regardless of whether traps were 12 or 50 m distant from the forest edge. The second group consisted of all the forest trap collections, regardless of whether traps were located on the forest edge or in the forest interior. Trap EE1 clustered with neither of the groups (Fig. 2). Separation of this trap community from the rest is undoubtedly due to the low number of butterflies collected ($n = 24$) relative to that collected from all other traps (85 ± 6.5 , mean \pm SE).

Habitat occurrence

Out of the 90 total butterfly species collected, 45 were represented by at least five individuals and could be quantified for relative habitat occurrences (Fig. 3). Out of these 45 species, 15 were trapped in a single broad habitat type; nine were trapped only in the forest (edge and interior combined) and six were trapped only in the matrix (far and near combined). Two-thirds of the species (30 out of 45)

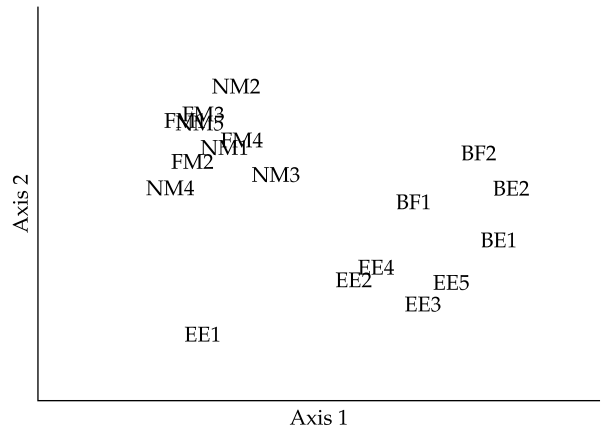


Fig. 2. Non-metric multidimensional scaling ordination of trap collections of fruit-feeding butterflies. Trap collections that are closer together are more similar to each other and vice versa. Points indicate trap locations coded by habitat (first and second positions: BE, Bossart-edge; BF, Bossart-forest; EE, Elbers-edge; NM, near matrix; FM, far matrix;) and trap number (third position: BE and BF have only two traps each, all others have five).

occurred in both matrix and forest habitats, although 78% were predominately trapped ($\geq 80\%$ occurrence) in one or the other of these habitats.

Only 2 out of the 45 species are GUI specialists (*Bicyclus safitza* Westwood and *Hamanumida daedalus* Fabricius (Nymphalidae)), and two others are considered UBQ (*Melanitis leda* Linnaeus and *Byblia anvatara* Aurivillius (Nymphalidae) Larsen *et al.* 2007). The remaining 41 are forest-associated species. Out of these, 63% (26 out of 41) are forest generalists and found in all forest subtypes. The other 37% are forest habitat specialists; 7% (3 out of 41) are predominately associated with dry forests and 29% (12 out of 41) are centred on wet or moist forests. No SUD species were collected, which was expected since this habitat is found only in the far north of the country, well outside the forest zone where the study was conducted.

There was no linkage between the habitat occurrences of species, i.e. where they were trapped, and their predetermined habitat associations (Fig. 4). Strong association would be apparent as an overall progressive decrease in dark to light shading moving from top to bottom on the graph, indicating a decreasing occurrence in forest habitat traps by species that have an increasingly loose association with wetter forests. However, out of the 41 forest species trapped, WEF or MEF species accounted for only a slightly higher percentage of those collected predominately in forest habitat *versus* those commonly trapped in the matrix (37 *vs.* 23%), and this difference was not statistically significant ($\chi^2 = 0.97$; $P = 0.32$). Additionally, the 26 forest generalists that were

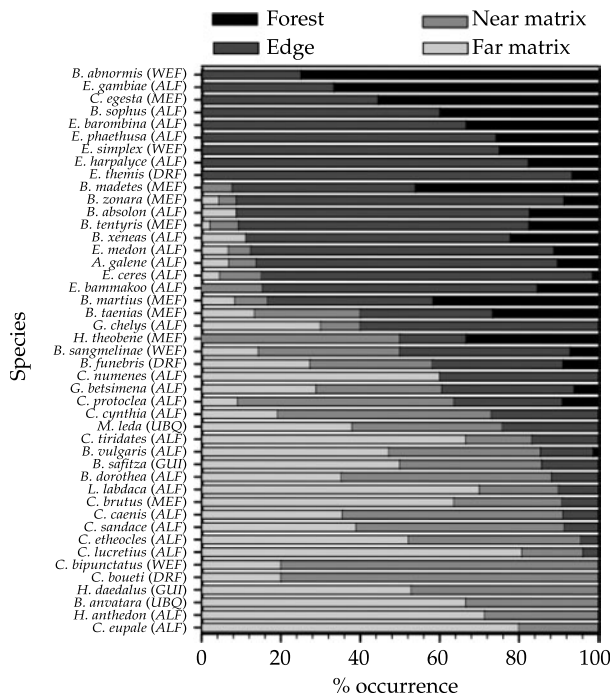


Fig. 3. Percentage occurrence of 45 fruit-feeding butterfly species in four habitat types. Species are ordered with respect to their increasing occurrence in the matrix (near and far combined). Species trapped only in forest are additionally ordered with respect to their increasing occurrence in edge habitat; similarly, species trapped only in matrix are additionally ordered with respect to their increasing occurrence in far matrix. See Appendix 1 for full names of genera.

trapped spanned the spectrum of relative habitat occurrences, from those trapped only in the forest to those trapped only in the matrix. DRF species were expected to have high tolerance of the drier conditions outside the forest, but the very common DRF species, *Euphaedra themis* Hübner (Nymphalidae), was never trapped in the matrix.

Discussion

Fruit-feeding butterfly communities trapped in forest habitats were distinct from those trapped in the surrounding farm bush savannah. Since rarefied species richness was broadly similar across habitats, these differences mostly reflect differences in species composition within communities and relative abundances of shared species. Studies of beetles (Spector and Ayzama, 2003), spiders (Vandergast and Gillespie, 2004) and mammals (Bentley *et al.*, 2000) have also reported differences in diversity between forest and matrix communities. Kotze and Samways (1999) found that Afromontane forests harboured communities of

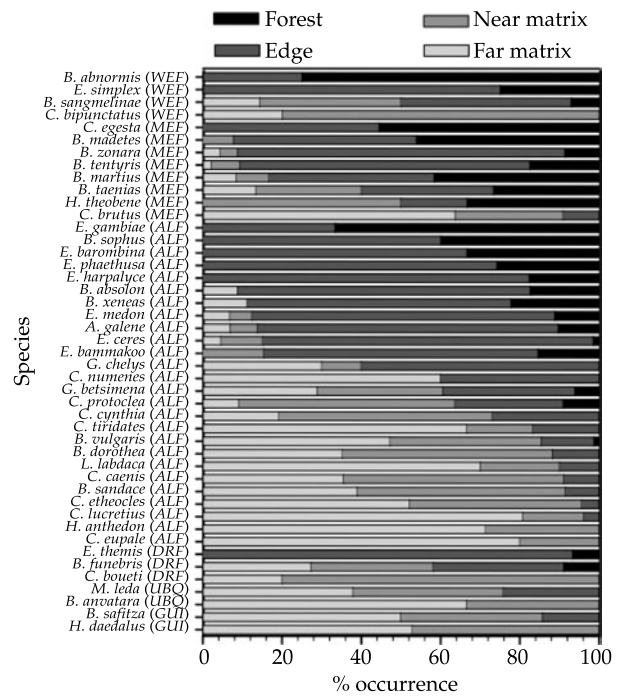


Fig. 4. Correspondence between the habitat associations of 45 fruit-feeding butterfly species and their percentage occurrence in four habitat types. Species are ordered with respect to their increasingly loose association with wetter forests and following the relationship predicted a priori for their presumed fidelity to moist forest habitat: WEF, wet forest species; MEF, moist forest species; ALF, species found in all forest subtypes; DRF, dry forest species; UBQ, ubiquitous species; and GUI, guinea savannah species. Habitat associations follow Larsen *et al.* (2007). Within each habitat association category, species found only in forest are additionally ordered with respect to their increasing occurrence in edge habitat; similarly, species found only in matrix are additionally ordered with respect to their increasing occurrence in far matrix. See Appendix 1 for full names of genera.

carabids and ants that were distinct from those of the surrounding grassland matrix, but also determined that edge communities of ants shared greater similarity with grassland communities than with forest communities. In our case, edge communities of butterflies were most similar to those deeper in the forest *versus* those outside the forest, but only a few genuine savannah-dwelling species are attracted to fruit-baited traps (indeed, we only collected 2 of 82 possible), and our trap captures were almost entirely forest species. Consequently, differences we observed between matrix and forest communities mostly reflect which forest-dwelling species were willing to leave the forest *versus* those that were not. Had we not focused only on the fruit feeders, relative distinctions among communities trapped in the matrix, edge or forest may have

differed from those observed here. Edge and matrix collections, for example, might have been more closely aligned. Horner-Devine *et al.* (2003), however, found very similar patterns between fruit feeders and non-fruit feeders. That there were additionally no differences among trap communities within each of these broader habitat types, e.g. trap communities at 12 m were not different from those at 50 m, implies that (1) butterflies leaving the forest are just as likely to move 50 m into the matrix as 12 m, and (2) edge habitat is generally perceived as forest by fruit-feeding butterflies at the distances investigated here.

Ten species showed very high fidelity to forest habitat (<20% occurrence in the matrix) and only another nine showed strict fidelity, i.e. were never found in the matrix. This is good news from a conservation perspective. Given that movement out of the forest is a necessary first step for dispersal across the matrix, the fact that more than half of the forest-associated butterflies collected were commonly trapped in the matrix suggests that many of these have at least the potential to be resistant to forest fragmentation and land use change. A matrix that is a mixed mosaic of land cover and land use types can have significant conservation value to the extent it presents a relatively benign environment, promotes connection among populations in separate habitat patches and supplements or provides needed resources (Gascon *et al.*, 1999; Ricketts *et al.*, 2001; Daily *et al.*, 2003; Dennis *et al.*, 2003; Horner-Devine *et al.*, 2003; Marín *et al.*, 2008; Perfecto and Vandermeer, 2008). Which, if any, of the species we trapped in the matrix had literally moved out of Bobiri forest as opposed to dispersing from elsewhere within the matrix is unknown. However, only that subset of species that consists of strong dispersers or that does not have an obligate association with forest resources would ultimately be expected to successfully disperse away from a forest fragment, whether it is Bobiri forest or another. Physically, the *Charaxes* Ochseneimer (Nymphalidae) are the most likely candidates capable of movement between fragments because they are large, robust-bodied and strong fliers. Bossart *et al.* (2006) often trapped these large butterflies in small, isolated, sacred forest groves even though these communities were overall much smaller and less diverse than those in forest reserves. Possibly, viable populations of these large butterflies reside and persist in these small patches. Alternatively, individuals may be dispersing across the landscape mosaic and passing through or recolonizing these forest remnants. Interestingly, not a single *Charaxes* was captured in the edge or forest traps during the current study. Their prevalence in these matrix traps combined with their presence in forest canopy traps

(J.L. Bossart, unpublished data) suggests that this group exhibits positive phototaxis and preferentially fly into the canopy upon reaching the boundary of large intact forests.

Nearly one-quarter of Ghana's forest butterfly species are habitat generalists found in all forest subtypes, but the other 75% tend to be specialists of either wet, moist or dry forest habitat (Larsen *et al.*, 2007). Although overlap of species among these ecological zones occurs, this overlap is largely in one direction. Species specialized on dry forest habitat are not uncommonly found in wetter forests in areas that are somewhat degraded or more open, but species associated with increasingly wet forests are much less rarely, if ever, found in dry forests. In light of this general pattern of habitat affinities, we expected that species centred on wet and moist forests would mostly be absent from the matrix and, conversely, that most ALF or DRF species would commonly be trapped in the matrix. Farm bush savannah intuitively seems more comparable to the environment of dry forests than to that of moist or wet forests. Generalists also by definition have a wider tolerance range and would presumably experience the landscape outside the forest as a less formidable challenge and may even rely in part on resources in the matrix. In fact, generalists are often considered less susceptible to extinction in human-dominated environments specifically because of their broader tolerances (Rabinowitz, 1981) and correlated broader distributions. However, contrary to our prediction, only 3 out of the 12 species associated with wetter forests were not trapped in the matrix; 5 out of the 12 were commonly trapped in the matrix. Perhaps more surprising, nearly half of the species that exhibited strong or complete fidelity to the forest were forest habitat generalists, and in one case, a dry forest specialist. The specific factors that account for the relaxed fidelity of forest species to forest habitat are unknown, but could include the lack of a behavioural aversion to heat, light, or decreased humidity or enhanced access to adult or larval resources located outside the forest (Dennis *et al.*, 2003; Fermon *et al.*, 2003). Additionally, at this point, we do not know how relative habitat fidelities are modified by seasonality or manifest in different taxonomic groups. Our matrix sampling occurred only during the wet season. In theory, species' fidelities could change temporally if patterns of resource distribution and availability between forest and matrix change across wet and dry seasons. Similarly, we focused only on the fruit-feeding butterflies. The percentages of species with stringent *versus* relaxed fidelity to forest habitats in lineages with markedly different resource requirements, e.g. ant-associated lycaenids, could differ from those we observed. Regardless of the factors

responsible and how these pan out seasonally and across taxonomic groups, responses will undoubtedly be species specific and modified by the relative hostility of the surrounding landscape. The current study represents an important but only a first step towards determining which forest-associated butterflies are resistant to forest fragmentation.

Conclusions

Our traps collected 45 fruit-feeding butterflies that could be quantified with respect to their habitat occurrence. Because the vast majority of these were forest-associated species, differences between forest and matrix communities identified which species were more *versus* less tightly linked to forest habitat. Slightly more than half of the forest species trapped were commonly collected in the matrix and therefore potentially able to move across the landscape. An unexpected result was the lack of any link between the known habitat affinities of species and their relative occurrence in forest *versus* matrix habitat. Species of wetter forests were no less likely to be trapped in the matrix than forest generalists or DRF species; conversely, some of the species most tightly linked to the forest were forest generalists or DRF species.

Acknowledgements

We wish to acknowledge the staff of the Bobiri Butterfly Sanctuary for their help and for making our stay an enjoyable and delightful experience. John Rawlins and his staff at Carnegie Museum of Natural History assisted with identification of difficult specimens. This research was supported by grants to J.L.B. from the National Science Foundation.

References

- Bender D. J., Contreas T. A. and Fahrig L. (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 79, 517–533.
- Bentley J. M., Catterall C. P. and Smith G. C. (2000) Effects of fragmentation of araucarian vine forest on small mammal communities. *Conservation Biology* 14, 1075–1087.
- Bossart J. L. and Opuni-Frimpong E. (2009) Distance from edge determines fruit-feeding butterfly community diversity in Afrotropical forest fragments. *Environmental Entomology* 38, 43–52.
- Bossart J. L., Opuni-Frimpong E., Kuudaar S. and Nkrumah E. (2005) Fruit-feeding butterfly communities of forest 'islands' in Ghana: survey completeness and spatial correlates of diversity. In *African Biodiversity: Molecules, Organisms, Ecosystems*, Proceedings of the 5th International Symposium on Tropical Biology, 2–6 May 2004, Museum Koenig, Bonn, Germany (edited by B. A. Huber, B. J. Sinclair and K.-H. Lampe), pp. 151–158. Springer Science, New York, USA.
- 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.
- Bossart J. L. and Pashley-Powell D. (1998) Genetic estimates of population structure and gene flow: limitations, lessons, and new directions. *Trends in Ecology and Evolution* 13, 171–212.
- Colwell R. K. (2005) EstimateS 7.5 User's Guide. <http://purl.oclc.org/estimates>
- Daily G. C., Ceballos G., Pacheco J., Suzán G. and Sánchez-Azofeifa A. (2003) Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* 17, 1814–1826.
- Dennis R. L. H., Shreeve T. G. and van Dyck H. (2003) Towards a functional resource-based concept for habitat: a butterfly biology view-point. *Oikos* 102, 417–425.
- Fairhead J. and Leach M. (2002) The dynamic forest landscapes of West Africa: their shaping in relation to natural and anthropogenic processes. In *Understanding and Capturing the Multiple Values of Tropical Forests* (edited by P. A. Verweij), pp. 21–35. Tropenbos International, Wageningen.
- Fermon H., Waltert M. and Mühlenber M. (2003) Movement and vertical stratification of fruit-feeding butterflies in a managed West African rainforest. *Journal of Insect Conservation* 7, 7–19.
- Gascon C., Lovejoy T. E., Bierregaard R. O. Jr, Malcolm J. R., Stouffer P. C., Vasconcelos H. L., Laurance W. F., Zimmerman B., Tocher M. and Borges S. (1999) Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91, 223–229.
- Gotelli N. J. and Entsminger G. L. (2003) Ecosim 7.00 User's Guide. <http://www.garyentsminger.com/ecosim/index.htm>
- Hall J. B. and Swain M. D. (1981) *Distribution and Ecology of Vascular Plants in Tropical Rain Forest: Forest Vegetation of Ghana*. W. Junk Publishers, The Hague. 383 pp.
- Horner-Devine M. C., Daily D. C., Ehrlich P. R. and Boggs C. L. (2003) Countryside biogeography of tropical butterflies. *Conservation Biology* 17, 168–177.
- Klein B. C. (1989) Effects of forest fragmentation on dung and carrion beetle communities in Central Amazonia. *Ecology* 70, 1715–1725.
- Kotze D. J. and Samways M. J. (1999) Invertebrate conservation at the interface between the grassland matrix and natural Afrotropical forest fragments. *Biodiversity and Conservation* 8, 1339–1363.
- Lande R. (1988) Genetics and demography in biological conservation. *Science* 241, 1455–1460.
- Larsen T. B. (2005) *Butterflies of West Africa*. Apollo Books, Svenborg. 865 pp.
- Larsen T. B., Aduse-Poku K., Boersma H., Sáfíán S. and Baker J. (2007) Bobiri butterfly sanctuary in

- Ghana – discovering its butterflies (with a checklist of the 930 butterflies of Ghana). *Metamorphosis* 18, 88–125.
- McCune B. and Grace J. B. (2002) *Analysis of Ecological Communities*. MJM Software Design, Gleneden Beach, Oregon. 300 pp.
- Magurran A. E. (2003) *Measuring Biological Diversity*. Blackwell Science Ltd, Malden, Massachusetts. 256 pp.
- Marín L., León-Cortés J. L. and Stefanescu C. (2008) The effect of an agro-pasture landscape on diversity and migration patterns of frugivorous butterflies in Chiapas, Mexico. *Biodiversity and Conservation* 18, 919–934.
- Perfecto I. and Vandermeer J. (2008) Biodiversity conservation in tropical agroecosystems: a new conservation paradigm. *Annals of the New York Academy of Science* 1134, 173–200.
- Pisces Conservation Ltd (2005) CAP 3.1. Pisces Conservation Ltd, New Milton.
- Poorter L., Bongers F., Kouamé F. N. and Hawthorne W. D. (2004) *Biodiversity of West African Forests: An Ecological Atlas of Woody Plant Species*. CABI Publishing, Cambridge, Massachusetts. 521 pp.
- Primack R. B. (2004) *A Primer of Conservation Biology* 3rd edn. Sinauer Associates Inc., Sunderland, Maryland. 320 pp.
- Rabinowitz D. (1981) Seven forms of rarity. In *The Biological Aspects of Rare Plant Conservation* (edited by H. Synge), pp. 205–217. Wiley, Chichester. 586 pp.
- Ricketts T. H. (2001) The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158, 87–99.
- Ricketts T. H., Daily G. C., Ehrlich P. R. and Fay J. P. (2001) Countryside biogeography of moths in a fragmented landscape: biodiversity in native and agricultural habitats. *Conservation Biology* 15, 378–388.
- Rosenblatt D. L., Heske E. J., Nelson S. L., Barber D. M., Miller M. A. and MacAllister B. (1999) Forest fragments in east-central Illinois: islands or habitat patches for mammals? *American Midland Naturalist* 141, 115–123.
- Sayer J., Harcourt C. S. and Collins N. M. (eds) (1992) *Conservation Atlas of Tropical Forests: Africa*. Macmillan Publishers Ltd, London. 74 pp.
- Spector S. and Ayzama S. (2003) Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian neotropical forest – savannah ecotone. *Biotropica* 35, 394–404.
- Vandergast A. G. and Gillespie R. G. (2004) Effects of natural forest fragmentation on a Hawaiian spider community. *Environmental Entomology* 33, 1296–1305.
- Villard M. A. (1998) On forest-interior species, edge avoidance, area sensitivity, and dogmas in avian conservation. *The Auk* 115, 801–805.
- Young A., Boyle T. and Brown T. (1996) The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution* 11, 413–418.

Appendix 1. Total specimens collected in traps in each habitat

Species	Habitats					Total trapped
	B-forest	B-edge	E-edge	Near matrix	Far matrix	
<i>Ariadne enotrea</i>	2	0	0	2	0	4
<i>Aterica galene</i>	3	3	19	2	2	29
<i>Bebearia abesa</i>	0	0	1	0	0	1
<i>B. absolon</i>	4	2	15	0	2	23
<i>B. cocalia</i>	0	0	0	1	0	1
<i>B. demetra</i>	1	0	0	0	0	1
<i>B. mandinga</i>	0	0	2	0	0	2
<i>B. mardania</i>	0	0	1	0	0	1
<i>B. paludicola</i>	0	0	2	0	0	2
<i>B. phantasina</i>	0	1	0	0	0	1
<i>B. sophus</i>	2	3	0	0	0	5
<i>B. tentyris</i>	17	17	54	7	2	97
<i>B. zonara</i>	2	0	19	1	1	23
<i>Bicyclus abnormis</i>	15	3	2	0	0	20
<i>B. dorothea</i>	0	0	2	9	6	17
<i>B. funebris</i>	13	24	24	45	40	146
<i>B. istaris</i>	0	0	1	0	0	1
<i>B. madetes</i>	6	1	5	1	0	13
<i>B. martius</i>	5	3	2	1	1	12
<i>B. procora</i>	1	0	0	0	0	1
<i>B. safitza</i>	0	2	0	5	7	14
<i>B. sandace</i>	0	1	4	31	23	59

Appendix 1. Continued

Species	Habitats					Total trapped
	B-forest	B-edge	E-edge	Near matrix	Far matrix	
<i>B. sangmelinae</i>	1	1	5	5	2	14
<i>B. taenias</i>	4	1	4	4	2	15
<i>B. vulgaris</i>	4	24	17	118	146	309
<i>B. xeneas</i>	2	3	3	0	1	9
<i>B. zinebi</i>	0	0	1	0	0	1
<i>Byblia anvatarata</i>	0	0	0	5	10	15
<i>Catacroptera cloanthe</i>	0	0	0	0	1	1
<i>Charaxes ameliae</i>	0	0	0	0	1	1
<i>C. anticlea</i>	0	1	0	1	1	3
<i>C. bipunctatus</i>	0	0	0	4	1	5
<i>C. boueti</i>	0	0	0	4	1	5
<i>C. brutus</i>	0	1	0	3	7	11
<i>C. castor</i>	0	0	0	0	1	1
<i>C. cynthia</i>	0	1	6	14	5	26
<i>C. etesipe</i>	0	0	0	0	1	1
<i>C. etheocles</i>	0	0	1	10	12	23
<i>C. eupale</i>	0	0	0	1	4	5
<i>C. lucretius</i>	0	1	0	4	21	26
<i>C. numenes</i>	0	2	0	0	3	5
<i>C. pleione</i>	0	0	0	1	0	1
<i>C. protoclea</i>	1	0	3	6	1	11
<i>C. tiridates</i>	0	0	1	1	4	6
<i>C. varanes</i>	0	0	1	1	0	2
<i>C. virilis</i>	0	0	0	0	1	1
<i>C. zingha</i>	0	0	1	0	0	1
<i>Cymothoe caenis</i>	0	0	4	25	16	45
<i>C. egesta</i>	5	3	1	0	0	9
<i>C. fumana</i>	0	1	0	0	0	1
<i>C. lurida</i>	0	0	0	1	0	1
<i>C. mabillei</i>	0	0	0	1	1	2
<i>Elymniopsis bammakoo</i>	2	8	1	2	0	13
<i>Euphaedra ceres</i>	1	4	51	7	3	66
<i>E. in anum</i>	1	1	0	0	0	2
<i>E. harpalyce</i>	3	1	13	0	0	17
<i>E. janetta</i>	0	0	1	1	0	2
<i>E. medon</i>	10	7	61	5	6	89
<i>E. modesta</i>	0	1	0	0	0	1
<i>E. phaethusa</i>	8	6	17	0	0	31
<i>E. sarcoptera</i>	0	0	1	0	0	1
<i>E. themis</i>	1	6	8	0	0	15
<i>Eurema hecabe</i>	0	0	0	1	0	1
<i>Euriphene amicia</i>	0	1	1	0	0	2
<i>E. ampedusa</i>	0	0	3	0	0	3
<i>E. aridatha</i>	2	0	0	0	0	2
<i>E. barombina</i>	3	1	5	0	0	9
<i>E. gambiae</i>	4	1	1	0	0	6
<i>E. simplex</i>	2	1	5	0	0	8
<i>Euryphura chalcis</i>	0	0	0	2	1	3
<i>Eurytela dryope</i>	0	0	0	1	1	2
<i>Gamia buchholzi/shelleyi</i>	0	0	1	0	0	1
<i>Gnophodes betsimena</i>	11	7	53	57	52	180
<i>G. chelys</i>	0	4	2	1	3	10
<i>Hamanumida daedalus</i>	0	0	0	8	9	17
<i>Harma theobene</i>	2	0	1	3	0	6

Appendix 1. Continued

Species	Habitats					Total trapped
	B-forest	B-edge	E-edge	Near matrix	Far matrix	
<i>Hypolimnas anthedon</i>	0	0	0	2	5	7
<i>H. misippus</i>	0	0	0	0	1	1
<i>H. salmacis</i>	0	0	2	2	0	4
<i>Junonia terea</i>	0	0	0	2	1	3
<i>Lachnoptera anticlia</i>	1	0	0	0	1	2
<i>Libythea labdaca</i>	0	0	1	2	7	10
<i>Melanitis leda</i>	0	3	11	22	22	58
<i>Melanitis libya</i>	0	0	3	0	0	3
<i>Neptidopsis ophione</i>	0	1	0	0	0	1
<i>Neptis metella</i>	0	0	0	0	3	3
<i>Palla decius</i>	0	0	0	1	0	1
<i>Palla ussheri</i>	0	0	1	0	0	1
<i>Pseudacraea lucretia</i>	1	1	0	0	0	2
<i>Hesperiidae</i> sp.	0	0	4	0	0	4