ECOTROPICA

EFFECTS OF TOPOGRAPHY ON FOREST BUTTERFLY ASSEMBLAGES IN THE PACIFIC LOWLANDS OF COSTA RICA

Hellena Binz[1,2]*, Christian H. Schulze[3] & Karl Eduard Linsenmair[1]

[1] Department of Animal Ecology and Tropical Biology, Theodor-Boveri-Institute,
University of Würzburg, Am Hubland, 97074 Würzburg, Germany

[2] Current address: Department of Evolutionary Biology,
University of Mainz, Johannes-von-Müller-Weg 6, 55128 Mainz, Germany

[3] Department of Tropical Ecology and Animal Biodiversity,
University of Vienna, Rennweg 14, 1030 Vienna, Austria

Abstract. Structural heterogeneity and plant composition of tropical rainforests are influenced by topography. By comparing butterfly richness and species composition of creek, slope, and ridge forest, we studied to what extent topography may also affect rainforest butterfly assemblages in Piedras Blancas National Park in the Pacific lowlands of southern Costa Rica (80–290 m a.s.l.). Butterflies were sampled by bait trapping and transect walks. Richness of fruit-feeding nymphalids sampled by bait trapping was highest in ridge forest, both at the forest site (mean richness) and forest type level (total richness). Butterfly assemblages sampled along transects were, in contrast, more speciose in creek forests, when considered at forest type level, while no significant differences were detected between forest types when analyzed on the level of forest sites. Species composition of bait-trapped nymphalids differed significantly between the three forest types, whereas this difference was less pronounced for butterflies sampled during transect walks. We therefore conclude that local butterfly richness in the Pacific lowlands of southern Costa Rica is shaped by small-scale topographic heterogeneity and probably mediated by microclimate, forest structure, and plant diversity. Rainforests on hilly terrain can be expected to maintain a more diverse butterfly fauna than rainforests on flat terrain.

Key words: biomass, functional groups, herbaceous vegetation, nitrogen, soil moisture, species diversity.

INTRODUCTION

Topographic variables play a primary role in explaining patterns of continental and regional-scale biodiversity (Coblentz & Ritters 2004, Davies *et al.* 2007) and can have prominent effects on vegetation structure on different spatial scales (Miyamoto *et al.* 2003, Fu *et al.* 2004). Tropical rainforests are the most complex terrestrial ecosystems, which show, even on small spatial scales, highly variable structure and species composition, which contributes via positive feedback to the high local and regional plant diversity (Gentry 1988a, 1988b; Chen *et al.* 1996, 1999;

Whitmore 1998, Clark *et al.* 1999, Clark & Clark 2000, Weissenhofer *et al.* 2008). In tropical rainforests on hilly terrain, the transitions from ridges through slopes to sites near watercourses represent important environmental gradients for plants (Kahn 1987, Gibbons & Newbery 2002). Particularly the changes in microclimate and soil, which are the main determinants for plant species composition (Chen *et al.* 1997), can be closely associated with local topographic gradients (Chen *et al.* 1999, Costa *et al.* 2005). Therefore topography may have a prominent effect on rainforest vegetation due to the creation of highly diverse micro-sites (Whitmore 1998, Valencia *et al.* 2004). The resulting small-scale spatial differ-

* e-mail: hellena.binz@gmx.de

ences in forest structure and the corresponding plant species composition are documented for several tropical regions (e.g. Kubota *et al.* 2004). Furthermore, these may also generate spatial differences in the animal assemblages associated with the respective plants (e.g. specialized herbivores; Basnet 1992, Webb *et al.* 1999, Fine *et al.* 2004).

The aim of this study was to analyze to what extent herbivorous insects are affected by topographic forest heterogeneity, using butterflies as model organisms. Butterflies are highly diverse in the floristically rich lowland tropics, the majority of species can be easily identified, and they are relatively well studied compared with other diverse arthropod taxa, due to their conspicuousness (New 1997), which makes them very attractive to many amateur scientists who have contributed tremendously to our knowledge. Therefore butterflies are particularly suitable for analyzing patterns of insect diversity and the effectiveness of conservation measures (DeVries *et al.* 1997, Grøtan *et al.* 2012). Hence butterflies have often been used as "flagship taxa" to quantify the conservation value of habitat types affected by human activities (Veddeler *et al.* 2005, Bobo *et al.* 2006, Ohwaki *et al.* 2007, Akite 2008).

This study was conducted at Piedras Blancas National Park in the Pacific lowlands of Costa Rica. The area is predominantly covered by tropical evergreen lowland forest. The hilly topography creates a high heterogeneity of forest types growing under different ecological conditions, such as microclimate and soil parameters (Weissenhofer *et al.* 2008). The forests exposed on ridge tops represent the driest and sunniest forest type and harbor the most speciose plant communities. Creek forests occur at the bottom of gorges, and are characterized by a permanently high humidity and much lower plant richness than ridge forests. Slope forests are intermediate between these two forest types with regard to plant richness and microclimate (Weissenhofer *et al.* 2008). We expect that these differences in microclimate, vegetation structure, plant richness and composition will also affect the local butterfly communities.

We analyzed to what extent butterfly assemblages differed in species abundance, richness, and composition between creek, slope, and ridge broadleaf forests in southern Pacific Costa Rica. In particular, we tested the following hypotheses:

(1) Plant species richness increases from creek to ridge forest (Weissenhofer *et al.* 2008). Due to the dependence of herbivores on their host plants, we expected a consequently higher butterfly species richness at ridge forest sites compared with creek forest sites.

(2) Because each of the studied forest types is characterized by a specific plant community (Weissenhofer *et al.* 2008), we expected that the local assemblage of herbivores, such as butterflies that depend on specific host plants, differs in species composition even more conspicuously between forest types than in species richness, resulting in distinct species assemblages.

To test our hypotheses we sampled butterfly assemblages over four months at six replicate sites per forest type, using the two sampling methods, fruit-bait trapping (Daily & Ehrlich 1995) and transect walks (Caldas & Robbins 2003).

METHODS

Study area and study sites. Fieldwork was conducted in the vicinity of the Tropical Research Station La Gamba (8°42'61"N, 83°12'97"W) in the Golfo Dulce region of the Pacific lowlands of south-western Costa Rica. The station is located at an elevation of 78 m a.s.l. at the edge of the Piedras Blancas National Park. With its 159 km² of pristine rainforest, this National Park represents, beside the Corcovado National Park on the Osa Pensinula, one of the last large Pacific lowland rainforest remnants of Central America. It harbors a huge amount of the country's biodiversity, for example about half of Costa Rica's butterflies (Wiemers & Fiedler 2008) and over three hundred bird species (Tebb 2008). The mean precipitation per year is 6000 mm, with a peak from August to November and a dry period between January and March. For more detailed information on geography, geology, and climate of the lowland rainforest of the Golfo Dulce region, see Weber & Baumgartner (2001).

The study sites were located in primary rainforest and represented three forest types: creek forest (CrF), slope forest (SlF), and ridge forest (RiF). All forest sites were connected by the surrounding old-growth broadleaf forest, so there were no obvious dispersal barriers for animals. Creek forest sites were located in creeks at elevations of between 80 and 123 m a.s.l. Ridge forest sites were located along the crest around the station at elevations of between 150 and 290 m a.s.l. Elevation of slope forest sites was between the other two forest types (136 to 175 m a.s.l). In each forest type butterflies were sampled by bait trapping and transect walks at the same six replicated sites
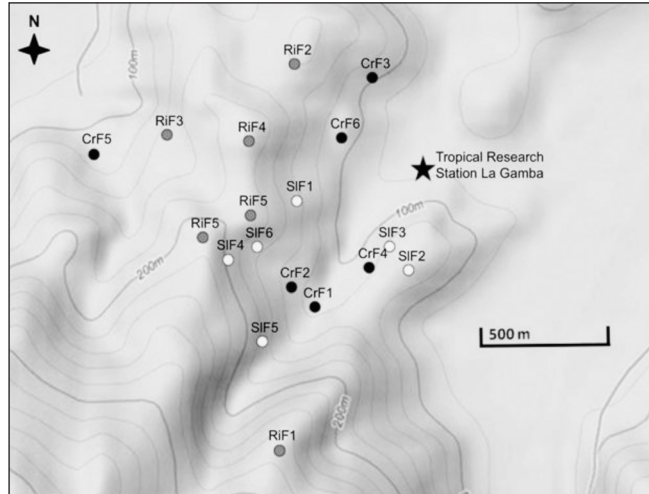
FIG. 1. Map of the study area near the Tropical Research Station La Gamba (8°42'61"N, 83°12'97"W), Costa Rica, indicating creek forest (CrF), slope forest (SlF), and ridge forest (RiF) sites.

(Fig. 1). Forest types were identified using a local vegetation map (Weissenhofer *et al.* 2008). Selected sites were distributed over approximately 1.5 km². Distances between sampled forest sites ranged between 110 and 1390 m and no spatial autocorrelation was found between forest types (ANOSIM: Global $R = 0.07$, $P = 0.18$).

Bait trapping of nymphalid butterflies. Fruit-feeding butterflies were sampled with 5 cylindrical gauze-traps (Daily & Ehrlich 1995) at each site. Traps were suspended from tree branches with string, with the bottom of the trap 1.00 m above the ground and at a distance of 5 to 10 m from each other along a linear transect. Strings were prepared with Tangle Foot™ glue, thus preventing ants from entering the traps. Additionally, all branches touching the traps were removed with a machete. Butterflies were baited with rotting bananas. Bait trapping was done on 30 days between 14 November and 24 December 2009 and on 25 days between 15 January and 25 February 2010. For each trapped butterfly species we collected at least one voucher specimen. All subsequently captured individuals were marked with a color pencil on the hindwings to avoid pseudoreplication due to recaptures, which can be particularly important in the case of long-living fruit-feeding nymphalid butterflies (Beck & Schulze 2000, Molleman *et al.* 2007). Marked butterflies were then released at the trapping site. In all our analyses, individuals trapped several times were only considered once.

Butterfly sampling by transect walks. In addition to bait trapping, which only allowed sampling of fruit-feeding nymphalid butterflies, we surveyed butterflies along transects on forest trails (Sparrow *et al.* 1994, Caldas & Robbins 2003). The surveys were carried out from 24 November to 24 December 2009 and from 14 January to 25 February 2010. Individual transects were 150 m long and were sampled 15 times for 10 min each between 08:00 and 16:00 h. Always at least one individual of each species was caught with a sweep net and identified by available literature (DeVries 1987, 1997). All subsequent individuals from conspicuous species, such as *Cissia hesione*, *Colobura dirce*, or *Peropthalma tullius*, were identified on the wing with the help of binoculars in the field. Therefore, in contrast to bait trapping, butterflies recorded during transect walks were not marked and might have been recorded multiple times. For each species, if possible, a minimum of one individual was collected or photographed as reference. Due to difficulties with identification, only the butterfly families covered by DeVries (1987, 1997) were considered in this study: Papilionidae, Pieridae, Nymphalidae, and Riodinidae.

Data analysis. One-way analyses of variance (ANO-VA), plus a subsequently calculated LSD post-hoc test and a multiple comparison of mean group ranks, were used to test for differences in butterfly abundance and species richness at sampling sites between forest types. All analyses were calculated with the software Statistica 8.0 (StatSoft, Inc. 2007).

Because of the short sampling period it was not possible to achieve complete species inventories. Therefore the recorded species represented only a fraction of the true species richness. Consequently, detected differences in recorded species numbers between forest types may be biased by the varying completeness of achieved species inventories due to different sample sizes (= number of sampled butterflies; Schulze *et al.* 2001). For this reason the Hurlbert rarefaction method (Krebs 1989) was applied, reducing the sample size for all three forest types to the largest shared number of sampled butterfly individuals. The resulting rarefaction curves allow a comparison of the expected number of species for a standardized sample size (Magurran 2004). Additionally, we calculated the 95% confidence intervals for each of the three resulting species detection curves.

Similarities of species assemblages between forest sites were quantified by Bray-Curtis similarities separately for bait traps and transect samples. Bray-Curtis similarities were calculated for all possible site pairings with the software Primer v5 (Clarke & Gorley 2001). Abundance data were square-root transformed to reduce the influence of dominant species. Similarities between sites are visualized in a non-metric multidimensional scaling (NMDS) plot (Clarke 1993). Stress values of < 0.20 indicate a reliable visualization of the similarity relationships by a NMDS ordination. On average, sites with higher similarity in species composition are plotted closer to each other than less similar sites. To test for effects of forest type on species composition, an analysis of similarity (ANOSIM) with 999 random permutations was conducted. To identify potential effects of a high proportion of rare species in our samples, we additionally calculated all ANOSIMs and NMDS ordinations after excluding all singletons in our bait trapping and transect samples.

RESULTS

Abundance and species richness. A total of 648 butterflies belonging to 95 species was recorded during a total of 36 bait-trapping days and 15 transect walks per study site (for species lists and numbers of sampled individuals, see Appendix 1). In the bait traps we caught a total of 141 individuals from 33 species of fruit-feeding nymphalid butterflies. A total of 507 butterflies representing 73 species was observed during transect walks. 51.5% and 38.4% of the species recorded during bait trapping and transect walks respectively were represented by singletons.

The mean number of individuals per bait-trapping site was significantly affected by the forest type (one-way ANOVA: $F_{2,15} = 5.60$, $p = 0.015$). The highest abundance of fruit-feeding nymphalid butterflies was recorded at RiF, which differed significantly from the other two forest types SlF and CrF (LSD test: $p < 0.05$; Fig. 2a). Also, abundance of butterflies recorded by transect walks was signifi-
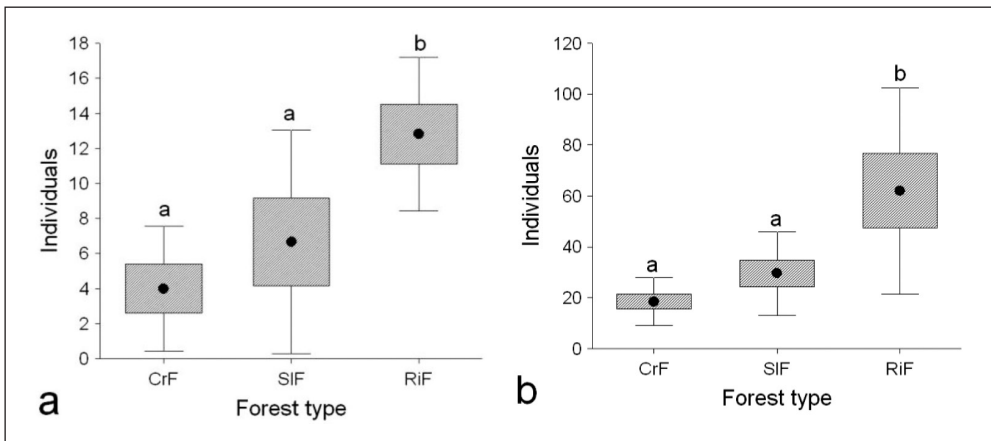

FIG. 2. Mean number of individuals ± SE (box) and 95% CI (whiskers) of (a) fruit-feeding nymphalid butterflies sampled by bait trapping and (b) butterflies observed along 150-m transects in creek forest (CrF), slope forest (SlF), and ridge forest (RiF; N = 6 sites per forest type). Different letters indicate significant differences between means (a: LSD test; b: multiple comparisons of mean group ranks).

FIG. 3. Mean number of species ± SE (box) and 95% CI (whiskers) of (a) fruit-feeding nymphalid butterflies sampled by bait trapping and (b) butterflies observed along 150 m transects in creek forest (CrF), slope forest (SlF), and ridge forest (RiF; N = 6 sites per forest type). Different letters indicate significant differences between means (a: LSD test; b: multiple comparisons of mean group ranks).
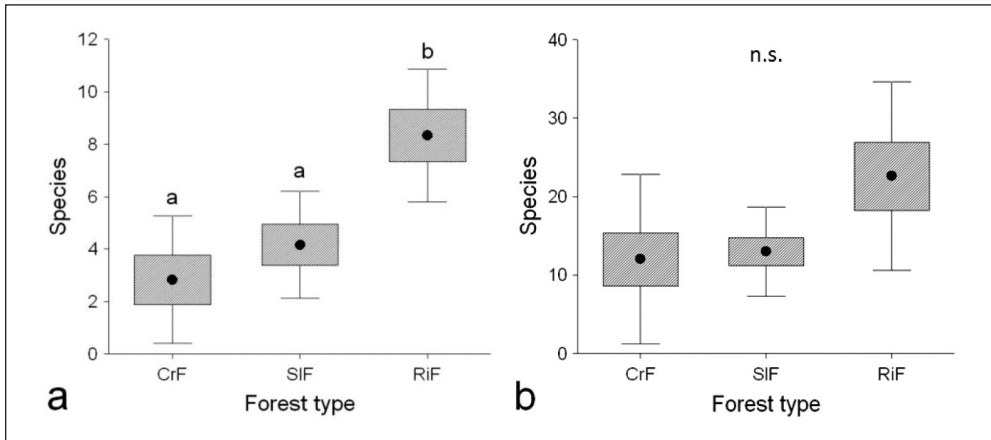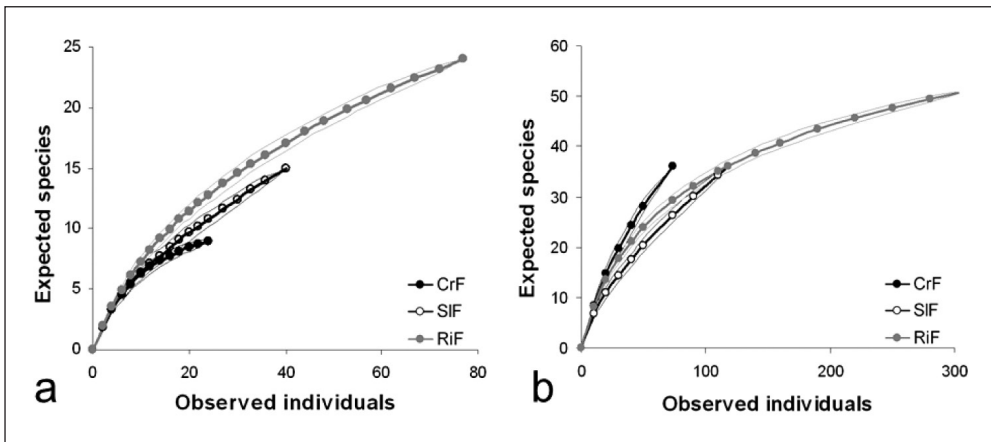

FIG. 4. Rarefaction curves (± 95% CI) showing species accumulation for (a) fruit-feeding butterfly species sampled by bait trapping and (b) butterflies sampled along 150-m transects in creek forest (CrF), slope forest (SlF), and ridge forest (RiF).

cantly affected by forest type (one-way ANOVA: $F_{2,15}$ = 4.99, P = 0.031). Again, the highest numbers of butterflies were observed at RiF sites and significantly lower abundances at CrF and SlF (multiple comparison of mean group ranks: P < 0.05; Fig. 2b).

Mean total species numbers recorded per study site also differed significantly between forest types in fruit-feeding nymphalids (one-way ANOVA: $F_{2,15}$ = 9.88, P = 0.002), but not in butterflies recorded during transect walks (one-way ANOVA: $F_{2,15}$ =

2.87, P = 0.1). However, both sampling methods revealed highest mean species richness at RiF sites and lower richness at SlF and CrF sites (Fig. 3).

Moreover, also species accumulation curves showed significantly higher species richness of fruit-feeding nymphalid butterflies for RiF than for SlF and CrF sites, as indicated by the non-overlapping 95% CIs. CrF showed lowest species richness (Fig. 4a). In contrast, species accumulation curves (with their 95% CIs) for butterflies sampled by
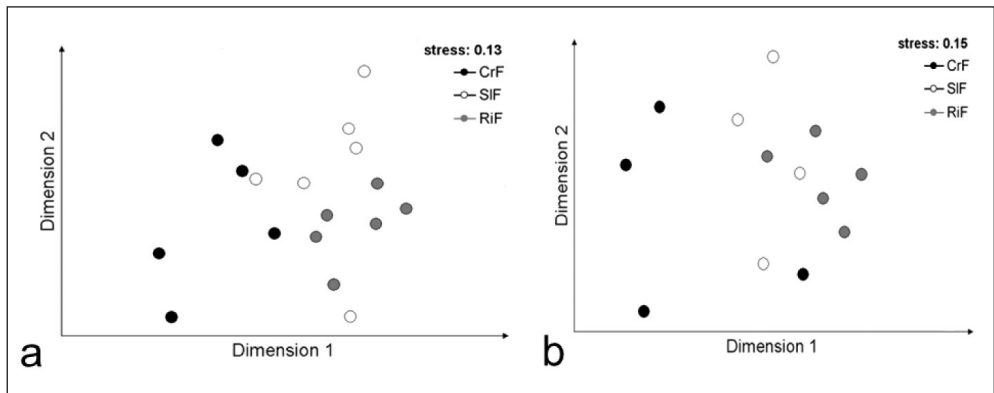
FIG. 5. NMDS ordination plot (based on Bray-Curtis similarities) for (a) fruit-feeding nymphalid butterflies sampled by bait trapping and (b) butterflies observed during transect surveys at creek forest (CrF), slope forest (SlF), and ridge forest (RiF) sites.

transect walks indicate higher species richness at CrF sites compared with the other two forest types (Fig. 4b).

Species composition. A NMDS plot based on Bray-Curtis similarities shows a clear segregation of CrF, SlF and RiF sites, indicating site-specific assemblages of fruit-feeding nymphalid butterflies. Only the species composition at SlF 2 deviated from this pattern for unknown reasons (Fig. 5a). Only five CrF sites are plotted, because no butterflies were caught at one of them. The NMDS plot also indicates a segregation into forest types for the butterfly assemblages sampled during transect walks (Fig. 5b). NMDS ordinations of bait traps and transect samples showed a very similar pattern when excluding singletons (not shown).

One-way ANOSIMs performed on the Bray-Curtis similarity matrices to test for effects of forest type on species composition showed significant differences between forest types in bait trap samples (Global R = 0.38, P = 0.001; without singletons: Global R = 0.37, P = 0.001) and transect walk samples (Global R = 0.38, P = 0.005; without singletons: Global R = 0.30, P = 0.001). With both sampling methods significant differences were found between almost all three forest types, with the exception of the pairwise comparison of Bray-Curtis similarities of the assemblages from transect walks at CrF and SlF (Table 1). Bray-Curtis values were neither correlated with distances between bait-trapping sampling sites (Spearman matrix rank correlation; Rho = -0.168, P = 0.9; without singletons: Rho = -0.146, P = 0.87) nor with distances between transect sites (Rho = 0.112, P = 0.25; without singletons: Rho = -0.041, P = 0.36), indicating that similarities found are not significantly biased by spatial autocorrelation.

DISCUSSION

We found higher butterfly abundance (both sampling methods) and species richness (only bait-trapping samples) at ridge forest sites than in creek and slope forest. Several reasons could account for these results. First, ridge forests represent the forest type with the highest floristic diversity in our study region (Weissenhofer *et al.* 2008). This higher plant diversity might mean a higher diversity of larval host plants and/or a higher abundance of adult butterflies in search for adequate oviposition sites (Murdoch *et al.* 1972, Novotny *et al.* 2006).

Second, at least some butterflies may reach higher abundances at ridge forest sites during their search for potential mates. A substantial proportion of Papilionidae, Pieridae, and Nymphalidae species use hilltops as landmarks for patrolling in search for mates (Shields 1967, Alcock 1983, 1985; Navez & Ishii 2007).

Furthermore, the more open forest structure at ridge forests may allow butterflies that are otherwise restricted to the canopy layer to also enter the lower forest strata. Butterfly assemblages usually show a clear vertical stratification in natural forest (DeVries *et al.* 1997, 1999, 2012; Schulze *et al.* 2001), which may partly disappear, e.g., following forest disturbance (Fermon *et al.* 2003, 2005). Perhaps similar

TABLE 1. Results of analyses of similarity (ANOSIMs) testing for effects of forest type (CrF = creek forest, SlF = slope forest, RiF = ridge forest) on the composition of fruit-feeding nymphalid butterflies and butterflies observed during transect surveys at individual sampling sites. ANOSIMs were calculated once including all species and then again excluding species only recorded as singletons. Faunal similarity was quantified by Bray-Curtis similarities, based on square-root-transformed abundances.

Pairwise comparisons	Bait trapping	Transect walks
All species		
CrF vs. RiF	$R = 0.65$, $P = 0.002$	$R = 0.64$, $P = 0.029$
CrF vs. SlF	$R = 0.31$, $P = 0.024$	$R = 0.32$, $P = 0.063$
RiF vs. SlF	$R = 0.23$, $P = 0.022$	$R = 0.34$, $P = 0.048$
Excluding species only recorded as singletons		
CrF vs. RiF	$R = 0.67$, $P = 0.002$	$R = 0.52$, $P = 0.020$
CrF vs. SlF	$R = 0.33$, $P = 0.017$	$R = 0.12$, $P = 0.145$
RiF vs. SlF	$R = 0.21$, $P = 0.045$	$R = 0.25$, $P = 0.019$

situations may occur at ridge forest sites. Due to the topography, a clear vertical stratification of vegetation layers may be less pronounced at ridge forest than at, e.g., creek forest sites. This makes it easier for canopy species to penetrate the lower forest strata. In consequence, the butterfly assemblage in the understory of ridge forest might be characterized by a mixture of understory and canopy butterfly species, which may contribute to the higher abundance and species richness found at ridge forest sites. However, only fruit-feeding nymphalid butterflies sampled by bait trapping reached a higher species richness at ridge forest sites. Species richness of butterflies sampled during transect walks did not differ significantly between forest types at the level of study sites, though richness showed a slight increase in creek forest compared with the two other forest types when samples were pooled at the level of forest types. The reasons for this pattern remain unclear.

In our study, a stronger effect of forest type was found on species composition than on species richness of butterfly assemblages. Both sampling methods indicated pronounced differences in butterfly species composition between all three forest types. A strong topographic heterogeneity effect was also found in an Amazonian lowland rainforest, where the species composition of ant assemblages differed significantly between forest plots in valleys and on ridges (Vasconcelos *et al.* 2003). Other studies have also demonstrated that habitat heterogeneity has a much stronger effect on β-, than on α-diversity (Kessler *et al.* 2009). This may also be valid for the heterogeneity of different lowland forest types, as indicated by our data on butterflies.

Species composition of forest understory butterflies may be shaped by a variety of abiotic and biotic factors, such as microclimate, understory structure and density as well as plant species composition. For our study area, differences in understory densities and plant composition among forest types were described by Weissenhofer *et al.* (2008). These differences certainly have species-specific effects on butterflies in terms of availability of adequate resources for larvae and adults in different forest types. Changes in species assemblages due to differences in vegetation structure were also found for butterflies in selectively logged forest (Hamer *et al.* 2003)

The high proportion of singletons in our samples indicates that sampling effort may be a limitation of our dataset. In fact, many butterfly studies, including ours, were conducted over relatively short time periods, which can limit comparisons among community subsets due to seasonal changes in species richness and species similarity (DeVries *et al.* 2012, Grøtan *et al.* 2012). Unfortunately, this problem cannot be avoided in many studies due to limited time for fieldwork. However, even an exclusion of all singletons from our dataset provided very similar results for bait-trapping and transect samples. Therefore we conclude that the detected differences in species composition between forest types are robust against the obvious undersampling of the species assemblages.

CONCLUSIONS

A study on North American swallowtail butterflies showed that patterns of species richness are partly related to large-scale topographical heterogeneity (Kerr *et al.* 1998). Our results clearly demonstrate that topographical heterogeneity may also shape butterfly richness on much smaller spatial scales. The three lowland forest types within our small study area of approximately 1.5 km² differed in their respective butterfly species compositions. Therefore topography contributed substantially to the local species pool. This underlines the overarching role of forest heterogeneity for shaping patterns of lowland forest diversity and has important implications for the design of insect surveys in tropical forests. In order to collect reliable information on the local forest arthropod fauna, surveys have to consider the area's topographical heterogeneity when estimating the effort necessary for achieving a high completeness in species inventories. Also, conservation efforts aiming to maintain a high fraction of the regional biodiversity should focus on areas characterized by high topographical heterogeneity which, consequently, harbor more forest types and associated species.

ACKNOWLEDGMENTS

REFERENCES

Akite, P. 2008. Effects of anthropogenic disturbances on the diversity and composition of the butterfly fauna of sites in the Sango Bay and Iriiri areas, Uganda: implications for conservation. African Journal of Ecology 46: 3–13.

Alcock, J. 1983. Territoriality by hilltopping males of the great purple hairstreak, *Atlides halesus* (Lepidoptera, Lycaenidae): convergent evolution with a pompilid wasp. Behavioral Ecology and Sociobiology 13: 57–62.

Alcock, J. 1985. Hilltopping in the nymphalid butterfly *Chlosyne californica* (Lepidoptera). American Midland Naturalist 113: 69–75.

Basnet, K. 1992. Effect of topography on the pattern of trees in Tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. Biotropica 24: 31–42.

Beck, J. & C.H. Schulze. 2000. Diversity of fruit-feeding butterflies (Nymphalidae) along a gradient of tropical rainforest succession in Borneo with some remarks on the problem of 'pseudoreplicates'. Transactions of the Lepidopterological Society of Japan 51: 89–98.

Bobo, K.S., Waltert, M., Fermon, H., Njokagbor, J. & M. Mühlenberg. 2006. From forest to farmland: Butterfly diversity and habitat associations along a gradient of forest conversion in Southwestern Cameroon. Journal of Insect Conservation 10: 29–42.

Caldas, A. & R.K. Robbins. 2003. Modified Pollard transects for assessing tropical butterfly abundance and diversity. Biological Conservation 110: 211–219.

Chen, J., Franklin, J. & S. Lowe. 1996. Comparison of abiotic and structurally defined patch patterns in a hypothetical forest landscape. Conservation Biology 10: 854–862.

Chen, Z.S., Hsieh, C.F., Jiang, F.Y., Hsieh, T.H. & I.F. Sun. 1997. Relations of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan. Plant Ecology 132: 229–241.

Chen, J., Saunders, S.C., Crow, T.R., Naiman, R.J., Brosofske, K.D., Mroz, G.D., Brookshire, B.L. & J.F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. BioScience 49: 288–297.

Clark, D.B. & D.A. Clark. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. Forest Ecology and Management 137: 185–198.

Clark, D.B., Palmer, M.W. & D.A. Clark. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. Ecology 80: 2662–2675.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117–143.

Clarke, K.R. & R.N. Gorley. 2001. PRIMER v5: User manual/tutorial. Primer-E, Plymouth, MA.

Coblentz, D.D. & K.H. Ritters. 2004. Topographic controls on the regional-scale biodiversity of the southwestern USA. Journal of Biogeography 31: 1125–1138.

Costa, F.R.C., Magnusson, W.E. & R.C. Luizao. 2005. Mesoscale distribution patterns of Amazonian understorey herbs in relation to topography, soil and watersheds. Journal of Ecology 93: 863–878.

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

Davies, R.G., Orme, C.D.L., Storch, D., Olson, V.A., Thomas, G.H., Ross, S.G., Ding, T.-S., Rasmussen, P.C., Bennett, P.M., Owens, I.P.F., Blackburn, T.M. & K.J. Gaston. 2007. Topography, energy and the global distribution of bird species richness. Proceedings of the Royal Society B 274: 1189–1197.

DeVries, P.J. 1987. The butterflies of Costa Rica and their natural history, Volume I: Papilionidae, Pieridae, Nymphalidae. Princeton University Press, Chichester, UK.

DeVries, P.J. 1997. The butterflies of Costa Rica and their natural history, Volume II: Riodinidae. Princeton University Press, Chichester, UK.

DeVries, P.J., Murray, D. & 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.

DeVries, P.J., Walla, T.R. & H.F. Greeney. 1999. Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. Biological Journal of the Linnean Society 68: 333–353.

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

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

Fermon, H., Waltert, M., Vane-Wright, R.I. & M. Mühlenberg. 2005. Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. Biodiversity and Conservation 14: 333–350.

Fine, P.V.A., Mesones, I. & P.D. Coley. 2004. Herbivores promote habitat specialization by trees in Amazonian forests. Science 305: 663–665.

Fu, B.J., Liu, S.L., Ma, K.M. & Y.G. Zhu. 2004. Relationships between soil characteristics, topography and plant diversity in a heterogeneous deciduous broad-leaved forest near Beijing, China. Plant and Soil 261: 47–54.

Gentry, A.H. 1988a. Tree species richness of upper Amazonian forests. Proceedings of the National Academy of Sciences, USA 85: 156.

Gentry, A.H. 1988b. Changes in plant community diversity and floristic composition on environmental and geographical gradients. Annals of the Missouri Botanical Garden 75: 1–34.

Gibbons, J.M. & D.M. Newbery. 2002. Drought avoidance and the effect of local topography on trees in the understorey of Bornean lowland rain forest. Plant Ecology 164: 1–18.

Grøtan, V., Lande, R., Engen, S., Saether, B.E. & P.J. DeVries. 2012. Seasonal cycles of species diversity and similarity in a tropical butterfly community. Journal of Animal Ecology 81: 714–723.

Hamer, K.C., Hill, J.K., Benedick, S., Mustaffa, N., Sherratt, T.N., Maryati, M. & V.K. Chey. 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.

Kahn, F. 1987. The distribution of palms as a function of local topography in Amazonian terra-firme forests. Experientia 43: 251–259.

Kerr, J.T., Vincent, R. & D.J. Currie. 1998. Lepidoptera richness patterns in North America. Ecoscience 5: 448–453.

Kessler, M., Abrahamczyk, S., Bos, M., Putra, D.D., Gradstein, S.R., Höhn, P., Orend, F., Pitopang, R., Saleh, S., Schulze, C.H., Sporn, S., Steffan-Dewenter, I. & T. Tscharntke. 2009. Alpha and beta diversity of plants and animals along a tropical land-use gradient. Ecological Applications 19: 2142–2156.

Krebs, C.J. 1989. Ecological methodology. Harper & Row, New York.

Kubota, Y., Murata, H. & K. Kikuzawa. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamic in a subtropical forest in Okinawa Island, southern Japan. Journal of Ecology 92: 230–240.

Magurran, A. 2004. Measuring biological diversity. African Journal of Aquatic Science 29: 285–286.

Miyamoto, K., Suzuki, E., Kohyama, T., Seino, T., Mirmanto, E. & H. Simbolon. 2003. Habitat differentiation among tree species with small-scale variation of humus depth and topography in a tropical heath forest of Central Kalimantan, Indonesia. Journal of Tropical Ecology 19: 43–54.

Molleman, F., Zwaan, B., Brakefield, P. & J. Carey. 2007. Extraordinary long life spans in fruit-feeding butterflies can provide window on evolution of life span and aging. Experimental Gerontology 42: 472–482.

Murdoch, W.W., Evans, F.C. & C.H. Peterson. 1972. Diversity and pattern in plants and insects. Ecology 53: 819–829.

Navez, S. & M. Ishii. 2007. Comparison of behavioral patterns of hilltopping butterflies on the summit, subsummit and slope of two mountains on the boundary between Osaka and Nara Prefectures, Central Japan. Transactions of the Lepidopterological Society of Japan 58: 127–144.

New, T.R. 1997. Butterfly conservation. Oxford University Press, Oxford.

Novotny, V., Drozd, P., Miller, S. E., Kulfan, M., Janda, M., Basset, Y. & G.D. Weiblen. 2006. Why are there so many species of herbivorous insects in tropical rainforests? Science 313: 1115–1118.

Novotny, V., Miller, S.E., Hulcr, J., Drew, R.A.I., Basset, Y., Janda, M., Setliff, G.P., Darrow, K., Stewart, A.J.A., Auga, J., Isua, B., Molem, K., Manumbor, M., Tamtiai, E., Mogia, M. & G.D. Weiblen. 2007. Low beta diversity of herbivorous insects in tropical forests. Nature 448: 692–695.

Ohwaki, A., Tanabe, S.I. & K. Nakamura. 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.

Schulze, C.H., Linsenmair, K.E. & K. Fiedler. 2001. Understorey versus canopy: patterns of vertical stratification and diversity among Lepidoptera in a Bornean rain forest. Plant Ecology 153: 133–152.

Shields, O. 1967. Hilltopping. Journal of Research on the Lepidoptera 6: 69–178.

Sparrow, H.R., Sisk, T.D., Ehrlich, P.R. & D.D. Murphy. 1994. Techniques and guidelines for monitoring neotropical butterflies. Conservation Biology 8: 800–809.

StatSoft, Inc.. 2007. STATISTICA (data analysis software system), version 8.0. www.statsoft.com

Tebb, G. 2008. The birds of La Gamba. Pp. 353–380 *in* Weissenhofer, A., Huber, W., Mayer, V., Pamperl, S., Weber, A. & G. Aubrecht (eds.). Natural and cultural history of the Golfo Dulce region, Costa Rica. Stapfia, Biologiezentrum des Oberösterreichischen Landesmuseums, Linz.

Valencia, R., Foster, R.B., Villa, G., Condit, R., Svennings, J.-C., Hernández, C., Romoleroux, K., Losos, E., Magårds, E. & H. Balslev. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. Journal of Ecology 92: 214–229.

Vasconcelos, H.L., Macedo, A.C.C. & M.S. Vilhena. 2003. Influence of topography on the distribution of ground-dwelling ants in an Amazonian forest. Studies on Neotropical Fauna and Environment 38: 115–124.

Veddeler, D., Schulze, C.H., Steffan-Dewenter, I., Buchori, D. & T. Tscharntke. 2005. The contribution of tropical secondary forest fragments to the conservation of fruit-feeding butterflies: effects of isolation and age. Biodiversity and Conservation 14: 3577–3592.

Webb, E.L., Stanfield, B.J. & M.L. Jensen. 1999. Effects of topography on rainforest tree community structure and diversity in American Samoa, and implications for frugivore and nectarivore populations. Journal of Biogeography 26: 887–897.

Weber, A. & T. Baumgartner. 2001. An introductory field guide to the flowering plants of the Golfo Dulce rain forests, Costa Rica: Corcovado National Park and Piedras Blancas National Park ("Regenwald der Österreicher"). Stapfia, Oberösterreichisches Landesmuseum, Linz.

Weissenhofer, A., Huber, W., Koukal, T., Immitzer, M., Schembera, E., Sontag, S., Zamora, N. & A. Weber. 2008. Ecosystem diversity in the Piedras Blancas National Park and adjacent areas (Costa Rica), with the first vegetation map of the area. Pp. 65–96 *in* Weissenhofer, A., Huber, W., Mayer, V., Pamperl, S., Weber, A. & G. Aubrecht (eds.). Natural and cultural history of the Golfo Dulce region, Costa Rica. Stapfia, Biologiezentrum des Oberösterreichischen Landesmuseums, Linz.

Whitmore, T.C. 1998. An introduction to tropical rain forests. Oxford University Press, Oxford.

Wiemers, M. & K. Fiedler. 2008. Butterfly diversity of the Piedras Blancas National Park and its vicinity – a preliminary assessment (Lepidoptera: Papilionoidea & Hesperioidea). Pp. 277–294 *in* Weissenhofer, A., Huber, W., Mayer, V., Pamperl, S., Weber, A. & G. Aubrecht (eds.). Natural and cultural history of the Golfo Dulce region, Costa Rica. Stapfia, Biologiezentrum des Oberösterreichischen Landesmuseums, Linz, Austria.

APPENDIX 1. Butterfly species and number of individuals recorded by bait trapping and transect walks at different forest types (CrF = Creek forest, SlF = Slope forest, RiF = Ridge forest).

FAMILY/Subfamily/	Bait trapping				Transect walks			
Species	CrF	SlF	RiF	Total	CrF	SlF	RiF	Total
NYMPHALIDAE								
Biblidinae								
Callicore lyca	-	-	-	-	-	1	3	4
Catonephele mexicana	-	1	-	1	-	-	-	-
Catonephele numilia	2	-	1	3	-	-	-	-
Eunica mira	-	-	-	-	-	1	2	3
Nessaea aglaura	1	7	11	19	2	1	4	7
Temenis pulchra	-	-	-	-	-	1	-	1
Charaxinae								
Archaeoprepona demophon	-	-	3	3	-	-	-	-
Consul fabius cecrops	-	-	2	2	-	-	-	-
Memphis beatrix	-	-	1	1	-	-	-	-
Memphis centralis	-	-	1	1	-	-	-	-
Memphis oenomais	-	1	-	1	-	-	-	-
Memphis proserpina	-	-	1	1	-	-	-	-
Memphis xenocles	-	-	3	3	-	-	-	-
Prepona omphale	-	-	1	1	-	-	-	-
Zaretis ellops	-	1	-	1	-	-	-	-
Cyrestinae								
Marpesia iole	-	-	-	-	1	-	-	1
Danainae								
Aeria eurimedia	-	-	-	-	-	1	6	7
Hyposcada virginiana	-	-	-	-	2	-	1	3
Lycorea cleobaea	-	-	-	-	1	1	-	2
Mechanitis lysimnia	-	-	-	-	1	-	-	1
Mechanitis polymnia	-	-	-	-	2	-	1	3
Heliconiinae								
Dryas iulia	-	-	-	-	-	-	1	1
Eueides lybia	-	-	-	-	2	7	9	18
Heliconius doris	-	-	-	-	-	-	1	1
Heliconius hecale	-	-	-	-	1	3	4	8
Heliconius hecalesia	-	-	-	-	-	-	2	2
Heliconius hewitsoni	-	-	-	-	1	2	13	16
Heliconius ismenius	-	-	-	-	-	-	1	1
Heliconius melpomene	-	-	-	-	1	-	-	1
Heliconius pachinus	-	-	-	-	-	1	12	13
Philaethria dido	-	-	-	-	-	-	7	7
Limenitidinae								
Adelpha boeotia	-	-	-	-	-	-	10	10
Adelpha cocala	-	-	-	-	-	-	6	6

FAMILY/Subfamily/	Bait trapping				Transect walks			
Species	CrF	SlF	RiF	Total	CrF	SlF	RiF	Total
Adelpha heraclea	-	-	-	-	-	-	1	1
Adelpha iphiclus	-	-	-	-	-	-	3	3
Adelpha justina	-	-	-	-	-	-	1	1
Nymphalinae								
Anthanassa tulcis	-	-	-	-	-	-	1	1
Colobura annulata	-	-	1	1	-	-	-	-
Colobura dirce	3	9	11	23	-	2	4	6
Historis odius	-	1	-	1	-	-	-	-
Siproeta stelenes	-	-	-	-	2	-	4	6
Tigridia acesta	-	1	1	2	-	1	-	1
Satyrinae								
Antirrhea tomasia	6	-	-	6	10	2	-	12
Caligo eurilochus	-	-	1	1	-	-	-	-
Caligo memnon	-	-	1	1	-	1	2	3
Catoblepia orgetorix	-	-	1	1	-	1	-	1
Chloreuptychia arnaea	4	2	3	9	4	9	40	53
Cissia confusa	-	-	2	2	1	1	5	7
Cissia gomezi	-	-	1	1	-	1	5	6
Cissia hermes	-	-	-	-	1	1	22	24
Cissia hesione	2	3	3	8	1	-	3	4
Cissia libye	-	-	-	-	-	3	10	13
Cissia metaleuca	-	-	1	1	3	1	6	10
Cissia usitata	1	1	-	2	1	-	-	1
Cithaerias menander	-	-	-	-	-	15	8	23
Eresia eutropia	-	-	-	-	1	1	3	5
Eresia mechanitis	-	-	-	-	1	-	-	1
Euptychia insolata	-	-	-	-	3	1	10	14
Euptychia jesia	-	-	-	-	-	3	19	22
Euptychia westwoodi	-	-	-	-	1	1	4	6
Megeuptychia antonoe	-	1	13	14	1	1	4	6
Morpho amathonte	4	-	-	4	2	-	2	4
Morpho peleides	1	1	4	6	-	1	-	1
Opsiphanes cassina	-	9	8	17	-	-	-	-
Opsiphanes invirae	-	1	-	1	-	-	-	-
Opsiphanes tamarindi	-	1	-	1	-	-	-	-
Pierella helvetia	-	-	-	-	8	10	20	38
Pierella luna luna	-	-	-	-	2	37	39	78
Taygetis penelea	-	-	-	-	1	-	-	1
Taygetis virgilia	-	-	1	1	-	-	-	-
PAPILIONIDAE								
Papilioninae								
Parides childrenae	-	-	-	-	-	-	2	2

FAMILY/Subfamily/	Bait trapping				Transect walks			
Species	CrF	SlF	RiF	Total	CrF	SlF	RiF	Total
Parides iphidamas	-	-	-	-	1	-	-	1
Parides lycimenes	-	-	-	-	-	-	1	1
PIERIDAE								
Coliadinae								
Eurema nise	-	-	-	-	-	-	3	3
RIODINIDAE								
Euselasiinae								
Euselasia aurantia	-	-	-	-	1	-	-	1
Euselasia aurantiaca	-	-	-	-	-	2	-	2
Euselasia procula	-	-	-	-	-	1	-	1
Riodininae								
Ancyluris jurgensenii	-	-	-	-	-	1	-	1
Chimastrum argenteum	-	-	-	-	-	-	1	1
Eurybia elvina	-	-	-	-	2	-	-	2
Eurybia lycisca	-	-	-	-	2	-	1	3
Eurybia unxia	-	-	-	-	1	-	-	1
Juditha molpe	-	-	-	-	-	-	1	1
Leucochimona lepida	-	-	-	-	-	-	1	1
Mesene phareus	-	-	-	-	-	-	1	1
Mesosemia asa	-	-	-	-	7	1	-	8
Mesosemia zonalis	-	-	-	-	2	-	2	4
Nymphidium ascolia	-	-	-	-	1	-	-	1
Peropthalma lasus	-	-	-	-	-	1	1	2
Peropthalma tullius	-	-	-	-	1	1	-	2
Pseudonymphidia clearista	-	-	-	-	-	-	1	1
Total abundance	24	40	77	141	74	119	314	507
Total species richness	9	15	24	33	36	36	51	73