

## HAWKMOTH DIVERSITY IN NORTHERN BORNEO DOES NOT REFLECT THE INFLUENCE OF ANTHROPOGENIC HABITAT DISTURBANCE

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Like in many other insect groups, species numbers of hawkmoths (Lepidoptera: Sphingidae) increase conspicuously from the temperate towards the equatorial regions. While for the total area of Europe 57 hawkmoth species are reported (Karsholt & Razowski 1996), on the island of Borneo alone at least 100 species occur (Schulze *et al.* 2000). Since sphingids can easily be recorded by light-trapping and are taxonomically well known (Kitching & Cadiou 2000), they have served as model organisms in a number of diversity studies (e.g., León-Cortés *et al.* 1998).

For the northern part of Borneo many quantitative light-trapping samples of hawkmoths from a wide variety of habitats and altitudes are available from Sarawak, Sabah and Brunei (Holloway 1976, Tennent 1991, Schulze 2000). Using this database, we analyzed the effect of anthropogenic habitat disturbance at the landscape level on diversity and species composition of hawkmoth ensembles sampled at lowland sites (< 600m a.s.l.). Habitat descriptions given in the sources allowed the sampling sites to be categorized either as locations with primary or old-growth forest nearby, or sites which only have secondary forest or cultivated areas in their vicinity. We expected that species diversity in the latter habitat types would be lower. Moreover, ensembles in more disturbed landscapes should differ in composition due to the preponderance of generalist species, while forest specialists should decrease or completely drop out.

To compare alpha diversity of hawkmoth samples between sites, we calculated the expected number of species for a largest shared sample size of 82 specimens (sites with fewer specimens were excluded, leaving 16 samples for analysis that represent a total of 4565 individuals in 66 species) by Hurlbert rarefaction (Hurlbert 1971). Rarefied species numbers were chosen for diversity comparisons, since sample sizes differed strongly (82–1480 individuals). Surprisingly, no significant differences in hawkmoth diversity were found between eight sites with and eight without primary forest (Mann-Whitney U-test:  $z = 0.525$ ,  $P = 0.645$ ). Only one site, situated in a cultivated area at the margin of Mount Kinabalu National Park (Sabah), held a significantly less diverse hawkmoth community (Fig. 1). Altitude had no significant effect on the diversity of hawkmoth ensembles in the lowland forest zone (Pearson correlation:  $r = -0.237$ ,  $P = 0.377$ ,  $n = 16$ ).

Beta diversity between hawkmoth samples was quantified by Gallagher's CNESS index (Trueblood *et al.* 1994, Legendre & Gallagher 2001), which is a metric version of the NESS index (normalized expected species shared; Grasse & Smith 1975). The optimal value of the sample size parameter  $m$  was determined as  $m = 20$  using the method suggested by Trueblood *et al.* (1994). The CNESS index is particularly useful for comparing samples of different sizes, or with different degrees of 'completeness', since this index explicitly takes sampling effects (e.g., representation of 'rare' species) into account. Mean faunal dissimilarity ( $\pm$  1SE) was  $0.994 \pm 0.043$  for all pair-

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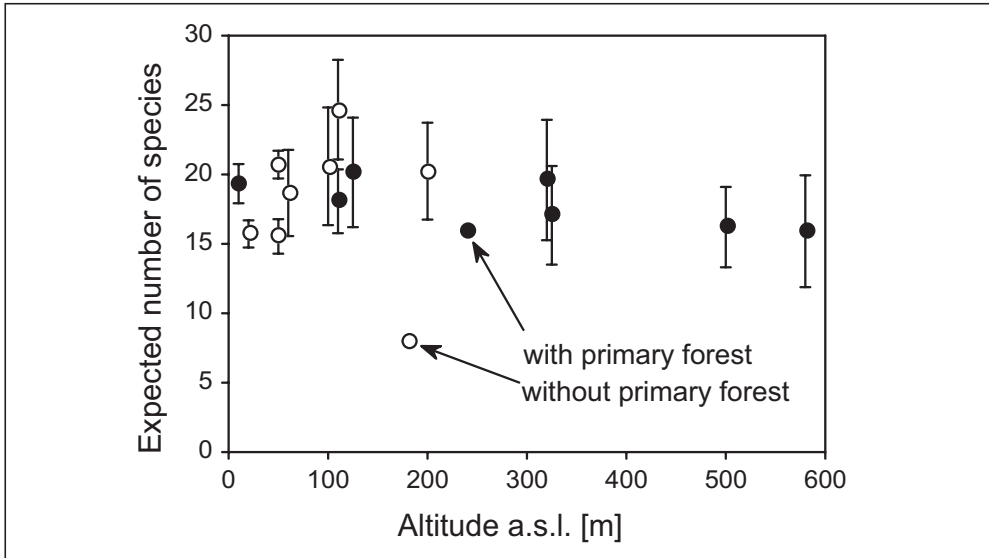


FIG. 1. Expected numbers of species for a largest shared sample size of 82 specimens (calculated by Hurlbert rarefaction)  $\pm$  95% confidence limits (after Simberloff 1978) for hawkmoth ensembles recorded quantitatively at different lowland sites in northern Borneo by light-trapping. [Open circles represent sites without, closed circles with primary forest.] Two sites had exactly 82 individuals sampled, so that species numbers have no variance estimates.

wise comparisons ( $n = 28$ ) between sites near old-growth forest,  $0.876 \pm 0.043$  ( $n = 28$ ) for disturbed landscapes, and  $0.953 \pm 0.028$  ( $n = 64$ ) for all pairwise comparisons between sites of both categories (note that CNESS attains a maximum dissimilarity value of 1.414). Differences between dissimilarities across the three types of pairwise comparisons were not significant (ANOVA:  $F_{2,117} = 2.025$ ,  $P = 0.137$ ). Moreover, when ordinating samples using non-linear multidimensional scaling (see Cox & Cox 1994) the two groups of sites showed strong overlap (Fig. 2). Two-dimensional ordination was deemed sufficient due to its moderate stress value (0.105; stress is a measure of goodness-of-fit in non-linear multidimensional scaling; Cox & Cox 1994), and the good fit between original data and distances in the ordination as revealed by a Shepard diagram (not shown; see Clarke 1993). A one-way MANOVA of the sample scores extracted from the two-dimensional ordination revealed no significant difference between the two groups of sites ( $F_{2,13} = 1.327$ ,  $P = 0.30$ ). Ordinations based on CNESS with  $m = 1$  (Orlóci's chord distance)

or  $m = 82$  (the maximum possible  $m$  value), as well as Soerensen index values (Wolda 1981) produced a very similar pattern (not shown).

These results indicate that many Bornean hawkmoth species are not closely bound to primary or old-growth forests and are relatively robust against anthropogenic habitat disturbance. This is in line with Holloway's earlier studies (e.g., Holloway 1984, 1993), although these did not include statistical analyses of the Sphingidae alone. Many hawkmoth species have the potential to behave as pioneers. This is not surprising taking into account the high mobility of most of these moths (except probably for some of the non-feeding Smerinthinae; Lemaire & Minet 1998). Moreover, for a large number of hawkmoths cultivated plants serve as larval food (e.g., Holloway 1987) or adult nectar sources (e.g., papaya). However, given the strong differences in resource use between adult hawkmoths (mostly nectarivores) and their corresponding larvae (herbivores), it remains to be tested whether records of adult moths away from forest are indicative of dispersal events only or really show successful coloniza-

tion of disturbed areas. Records of putatively rare species at heavily disturbed locations (e.g., *Clanis stenosema*, *Sataspes infernalis*; see Schulze *et al.* 2000) suggest that such habitats may even be important for those (specialized?) species. Of the 28 abundant species (represented by >25 individuals in the data base), only one (*Meganoton analis*) was confined to sites with old-growth forest nearby. As a cautionary note, however, it should be stressed that the results presented here only refer to nocturnal hawkmoths that can be monitored via light-trapping. We presently do not know whether our findings can also be extrapolated to diurnal or crepuscular species (e.g., many *Macroglossum* spp.).

Originally Borneo was almost completely covered by closed forest. In these pristine landscapes river banks and large tree-fall gaps may have played a central role as larval habitats for many hawkmoth species. Therefore, it can be assumed that a substantial proportion of Bornean hawkmoth species has benefited from clearing of forest areas and the wide variety of recently created secondary habitats, as long as these have not been totally converted into extended monocultural crop stands (e.g., oil palm plantations). Only a few

species like *Daphnusa ocellaris* show a clear preference for the understory of closed forest (Schulze 2000). Moreover, a comparison of hawkmoth ensembles between the canopy of primary dipterocarp forest and anthropogenically opened landscapes nearby revealed a remarkable similarity (Schulze 2000, Schulze *et al.* 2001), suggesting that a true canopy-specialist fauna is not that well developed among Bornean Sphingidae. Hawkmoths are thus an exceptional insect group, with many of their species being well adapted to survive in a changing environment dominated by cultivated areas and secondary forests. Therefore the usefulness of hawkmoths for monitoring or inventorying tropical insect faunas (e.g., as biodiversity indicators) is questionable. Even though planted or secondary forests can frequently hold a rather rich moth fauna, losses in diversity and changes in species composition are much more conspicuous for example in Geometridae or Pyraloidea (Chey *et al.* 1997; Intachat *et al.* 1997, 1999a, 1999b; Willott 1999; Schulze 2000; Beck *et al.* 2002) than among Sphingidae. Hence our results also point to the limitations in generalizing case studies from one taxon to another, or even in up-scaling to entire guilds.

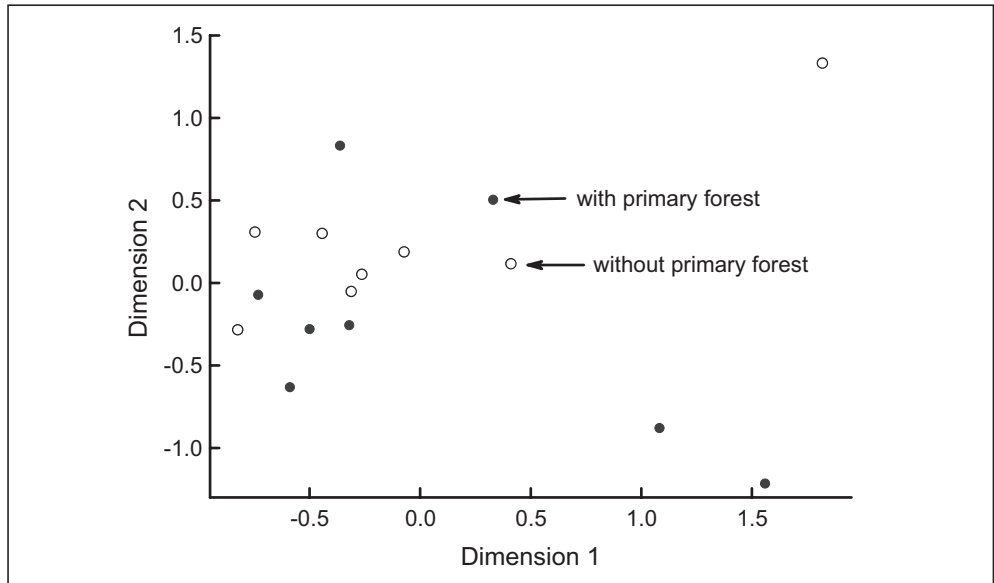


FIG. 2. Non-linear two-dimensional scaling plot of faunal dissimilarity based on CNESS ( $m = 20$ ) values. [Open circles represent sites without, closed circles with primary forest.]

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