Currently available data on Borneo geometrid moths do not provide evidence for a Pleistocene rainforest refugium

Jan Beck[1] & Cecil M. Rüdlinger

Abstract. Pleistocene climate led to lowered sea levels, which united land masses on the Sunda shelf. However, it remains uncertain whether this led to a unification of the rainforest habitats of these islands, or whether drier conditions restricted rainforest to mountainous refugial regions, with savannah belts separating forest blocks. Published data, such as within-species molecular analyses, community-wide analysis of similarity patterns, or peaks of known species richness and endemism, point towards the existence of separated refugial areas. However, sampling as well as publication bias might affect this perception, and more data from a variety of taxa are needed to evaluate the question thoroughly.

We used local samples of geometrid moths (Lepidoptera: Geometridae) from lowland primary forests in well-sampled north-eastern Borneo (within the suggested refugial area) and compared them to data from central Borneo (outside the purported refugial area). Higher local diversity in (hypothetical) refugial samples, and assemblage dissimilarities greater than what would be expected from distance decay alone, would be indications for an imprint of Pleistocene refugial history on these moth communities.

We did not find any such indications. There were neither significant differences in local diversity, nor in community turnover, between sites hypothesized to be refugial, and those not. However, the absence of proof is no proof of absence, and we discuss potentially confounding factors—such as dilution of community differences since the Pleistocene in this (probably) well-dispersing taxon, uncertainty in the exact limits of a refugial region, severe undersampling of (hypothetical) non-refugial areas, and statistical issues. More sampling in central and south-western Borneo will be necessary for a more thorough evaluation.

In Appendix we publish newly sampled quantitative data for geometrid moths from central Borneo. We report the first record of *Drapetodes interlineata* (Drepanidae) from Borneo.

Key words. biogeography, Camp Foyle, climate change, heart of Borneo project, Kalimantan Tengah

INTRODUCTION

Pleistocene history had a profound impact on species distributions in the Malay Archipelago (Lohmann et al., 2011). Glaciations at higher latitudes repeatedly lowered global sea levels by up to 120 m, exposing land bridges between continental shelf islands (Voris, 2000). As a consequence, today's separate regions on the Sunda shelf, i.e., the Malay Peninsula, Sumatra, Java, Bali and Borneo ("Sundaland"), were connected to each other. This has long been suspected (Wallace, 1869; Hall & Holloway, 1998; Beck et al., 2006) to be the cause of the remarkable similarity in species compositions on these islands, in comparison to the very different assemblages found on islands further to the east (without a history of Pleistocene land bridges). Shorter periods of higher sea levels than today also left a mark on species occurrences in the region (Woodruff & Turner, 2009; Woodruff, 2010).

However, another effect of Pleistocene climatic changes may also have impacted Sundaland, yet there is much less clarity on its extent and its effects on biomes. With cooler temperatures over tropical seas, the trade winds (i.e., the inner-tropical convergence zone) have weakened and monsoonal rains declined (Heaney, 1991; Morely, 2000). This led to a substantial reduction in rainfall across the Malay Archipelago, in particular in lowland regions. In consequence, it has been proposed that humid rainforests, which today would be the natural vegetation of most of Sundaland, have retreated into mountainous refugial regions such as the Barisan mountains of western Sumatra and the northeast of Borneo (Morely, 2000; Fig. 1). According to this scenario, Sundaland may have been connected by land yet its rainforest blocks were still separated by savannah regions. However, the evidence for such forest refugia is still scattered and inconclusive. Palynological evidence and fossils prove non-forest vegetation for some, and forests for other sites, but their punctuated distribution does not allow conclusions on corridors and connections between habitats. Vegetation models for the region, based on paleo-climatic reconstructions, are highly sensitive to initial parameterisation (Cannon et al., 2009) and therefore it remains uncertain whether Sumatran and Bornean forests were connected to each other or not.

[1]University of Basel, Department of Environmental Science (Biogeography), St. Johanns-Vorstadt 10, 4056 Basel, Switzerland; Email: jan.beck@unibas.ch (*corresponding author)
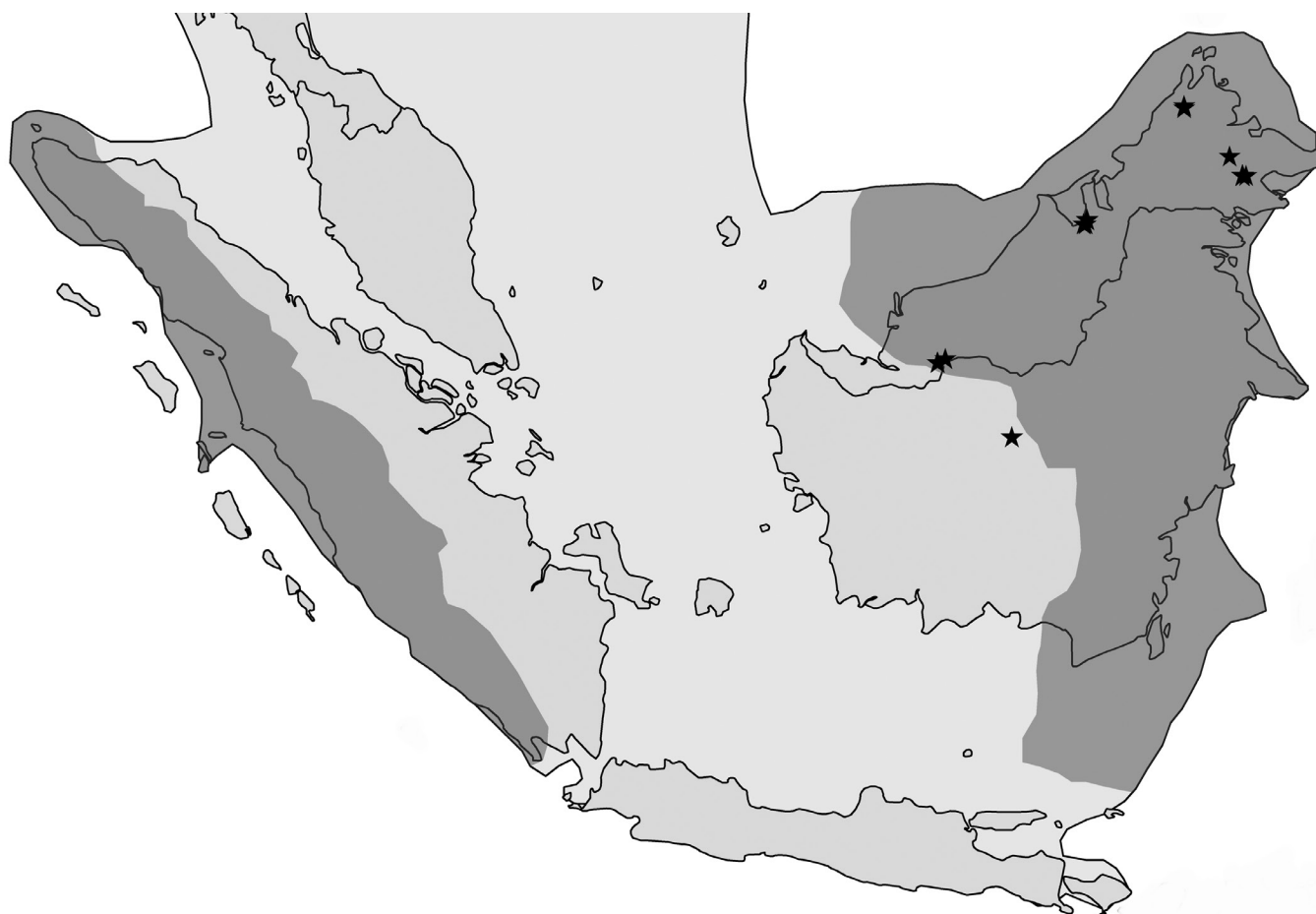
Fig. 1. Sundaland during the Pleistocene. Lowered sea levels exposed much of the Sunda shelf, unifying Borneo, Sumatra, Java, Bali and the Malay Peninsula. Today's coastlines and country borders are shown for orientation. Dark grey areas denote hypothesized rainforest refugia (redrawn from Gathorney-Hardy et al., 2002). Stars indicate sampling locations in Borneo as used for this study; the southern-most location is Camp Foyle (see Appendix for details).

The fact that, within Borneo, species records in the taxonomic literature are richest from the Malaysian state of Sabah (in the north-east), and hence observed diversity and endemism appear highest, seems to support the hypothesis of a north-eastern refugial area. However, Sabah also contains the island's highest mountain ranges (leading to many montane endemics, e.g., on Mt. Kinabalu; Luping et al., 1978). Furthermore, for logistical reasons, Sabah has been much more thoroughly studied than other regions of Borneo, particularly in comparison to the Indonesian part of the island (i.e., Kalimantan). Sampling effort can be a main determinant of perceived large-scale species richness patterns (Ballesteros-Mejia et al., 2013; Yang et al., 2013), so the impression that more species are known from the north-east could be deceiving. For trees, a taxon where systematic sampling has been carried out across the island, no north-eastern peak of diversity is evident (Slik et al., 2009).

Several studies reported potential effects of a rainforest refugium on species or communities in north-eastern Borneo. Gathorney-Hardy et al. (2002) found differences in assemblage compositions of termites between sites within and outside of supposed refugial areas across Sundaland. They interpreted this as imprints of Pleistocene history, arguing that the species of this poorly dispersing taxon have not yet fully spread into "newly" forested regions. On a population genetic level, forest-restricted species also supported the idea of refugial effects. For a species of forktail (*Enicurus leschenaultia*, a bird confined to the forest undergrowth), Moyle et al. (2005) reported data that suggest populations from western Sarawak (i.e., outside the refugium) had re-colonised the region from Peninsular Malaysia, rather than from (refugial) Sabah. Arora et al. (2011) and Locke et al. (2011) reported genetic separation times between the orang utan species of Borneo (*Pongo pygmeus*) and Sumatra (*P. abelii*) much longer ago than the last landmass unification of Sundaland, suggesting a dispersal barrier for these (mostly) arboreal apes.

However, there is a potential for publication bias against data that are not supportive of the refuge hypothesis, and only large, multi-taxon comparisons will allow a thorough evaluation of the evidence for refugial imprints on today's species and communities. In analogy, a long-debated refugial history of the Amazon rainforest is now seen as being based on evidence weakened by sampling bias (Colinvaux, 1989) and other confounding factors (Willis & Whittaker, 2000; Kricher, 2011).

Table 1. Results of linear models testing effects of refugial status of 33 sites (with and without accounting for effects of elevation) on two estimates of local diversity (Chao1, Fisher's α).

Response	Predictor(s)	Slope±SE	t	P
Chao1	Refuge [0,1]	22.50±43.35	0.519	0.607
Chao1	Refuge [0,1]	20.66±42.70	0.484	0.632
	Elevation [m]	0.20±0.14	1.411	0.169
Fisher's α	Refuge [0,1]	13.04±15.97	0.817	0.420
Fisher's α	Refuge [0,1]	12.60±16.02	0.786	0.438
	Elevation [m]	0.05±0.05	0.899	0.376

Table 2. Results of permutation tests (9999 runs) testing pairwise community similarity of 33 sites (as Jaccard index) for *(a)* effects of refugial status alone (Anosim), and *(b)* effects of refugial status corrected for spatial distance decay (partial mantel test). Using Morisita's index of similarity did not change conclusions (not shown).

Model type	Predictor(s)	Effect	P
Anosim	Refuge [0,1]	R = −0.240	0.965
Partial Mantel	Refuge [0,1]	r = 0.262	1.000
	Distance [m]	r = 0.513	0.001

In the present study we utilise data for a species-rich moth taxon (Lepidoptera, family Geometridae) to compare lowland rainforest communities from north-eastern and central Borneo. We investigate whether samples from central Borneo: (a) are less diverse on a local site level, compared to what is found in the north-east; and (b) whether there are substantially different local species communities found between the north-eastern and the central part of the island. Both aspects would point towards the reality of historical effects (i.e., a Pleistocene refugium) whereas there could be various reasons for not finding differences (see Discussion).

METHODS

Data sources. Data from local light trapping across north-eastern Borneo stem from a compilation by J. B., Chey V. K. (Sepilok, Malaysia) and J. D. Holloway (London, UK). This compilation has been the basis for various recent studies (e.g., Beck et al., 2011) and data were published with Beck et al. (2012). For the present study, we utilised only primary forest sites at elevations up to 430 m to facilitate comparisons with sites from lowland central Borneo. Despite this, the selected sites stem from a variety of natural forest habitats, e.g., different soil types (Holloway, 1984) and elevations that can add to variability in species communities (Beck & Chey, 2007, 2008; see Fig. 1 for map of localities).

Previously unpublished data from central Borneo were sampled during an expedition to Camp Foyle, a recently established research site on the foothills of the Schwaner mountains in Central Kalimantan (http://www.heartofborneo. org/), using similar field methods as for collecting data in northern Borneo. For four nights each, three sites in the vicinity of Camp Foyle (primary forest, 200 m a.s.l.) were sampled: directly at the Camp (structurally resembling a treefall-gap in the rainforest), in the dense understorey,

and in ca. 50 m height on an emergent tree (family Dipterocarpaceae).

Moths were attracted to weak (i.e., 15 Watt), battery-driven UV-light tubes placed inside a white gaze cylinder. Specimens were hand-sampled from dusk until midnight, pre-sorted to family level and identified based on the "Moth of Borneo"-series by Holloway (1986–2012). Only data for the family Geometridae were used for following analyses. Species of the closely related genera *Thallasodes* and *Pelagodes* cannot be reliably identified without male genitalic preparation, which was not feasible for this study. For comparability, we treated these problematic species on genus level for northern as well as southern datasets.

Analyses. Undersampling, i.e., not recording all species present in a habitat, is the rule in tropical entomology (Coddington et al., 2009). As undersampling heavily biases many metrics of assemblage similarity without viable options of numerically correcting for these (Beck et al., 2013), we first estimated the sample completeness of all sites as S_{obs}/S_{Chao}, where S_{obs} is the recorded species richness and S_{Chao} is the Chao1-estimate of species richness. We removed highly incompletely sampled sites ($S_{obs}/S_{Chao} < 0.3$) from analysis, leaving 30 sites from northern Borneo and 3 from the centre (most sites had $S_{obs}/S_{Chao} > 0.5$).

We measured the local diversity of sites based on Chao1-estimates of species richness and Fisher's α (see Beck & Schwanghardt, 2010, for their properties with regard to undersampling). General linear models were used to test for systematic effects of hypothetical refugial sites vs. non-refugial localities (i.e., northern vs. southern sites, Fig. 1), with and without controlling for elevation. Assumptions of linear, parametric models were fulfilled by data.

We calculated pairwise dissimilarity of sites based on Jaccard's and Morisita's indices. Jaccard's index utilises only information on presence or absence of species, which we consider appropriate for the biogeographic nature of our research question. However, Beck et al. (2013) showed high sensitivity of this type of metric to undersampling, so we used the abundance-based Morisita index (which is quite robust to undersampling) as a control to detect potentially remaining undersampling artefacts in our data.

We used permutation-based analysis of similarity (Anosim) to test for difference of dissimilarity patterns within and between sites of hypothetically different Pleistocene history (i.e., within and outside a refugium). If assemblages carry a historical signal, we expect refugial vs. non-refugial comparisons of sites to show higher dissimilarity than comparison between sites with the same history. Because dissimilarity is known to increase with distance in many taxa ("similarity decay"; Nekola & White, 1999; Hubbell, 2001), we also tested for historical signal (binary coded) with partial matrix correlations (Mantel test), using log-transformed distances as a covariate. Guillot & Rousset (2013) have recently pointed out some weaknesses of the Mantel test approach, but these are no reasons for concern in the light of our results. All analyses were carried out in R 2.15.2 (package vegan).

Some uncertainty persists towards the hypothetical refugial status of samples from Sarawak (north-western Borneo; Fig. 1 and Appendix). To assure that this does not lead to false conclusions, we repeated analyses without these samples.

RESULTS

Data from Camp Foyle (3 sites, see Appendix) were based on 605 individuals of 115 species (respectively genera for *Thallasodes/Pelagodes*, cf. Methods; see Appendix for data). The entire data set used for analyses (including northern samples, cf. Beck et al., 2012 for data) consisted of 8420 specimens from 33 lowland primary forest sites. The localities of sampling sites and their (hypothetical) refugial status are shown in Fig. 1.

We found no significant effects of refugial status on local diversity—neither for Chao1-estimates of species richness nor for Fisher's α (Table 1). These results were not affected by additional inclusion of (non-significant) positive effects of elevation on diversity (cf. Beck & Chey, 2008). Additional inclusion of sampling stratum as a covariate (forest canopy vs. understory, not shown) also did not affect model effects.

Results from matrix test of dissimilarities, with and without controlling for spatial distance, did also not indicate any significant historical signal in data (Table 2). Distance significantly affected dissimilarity patterns. Results based on Jaccard's index do not lead to different conclusions than those based on Morisita's index (not shown). I.e., an analytical focus on the more common species and their abundance relationships, which makes the analysis more robust to undersampling effects yet discards information on

rare species distributions, also did not indicate differences that could be related to history.

The exclusion of 15 northern-western sites (i.e., Lantiak-Entimau, Gunung Mulu; Appendix) also did not change conclusions (not shown in all detail). Results for partial Mantel test, for example, indicate no effect of Pleistocene history (r =−0.255, p =0.974) and a strong effect of spatial distance (r = 0.666, p = 0.001).

DISCUSSION

Our analyses of geometrid moths from 33 lowland primary rainforest sites did not indicate any effects that could be related to a Pleistocene rainforest refugium in north-eastern Borneo. Neither did local diversity differ significantly between sites within and outside the suggested refugial region, nor did we find a corresponding shift in the compositional similarities of assemblages. However, while patterns supporting a Pleistocene refuge would have been supportive of the refugial hypothesis, the absence of such evidence in our data cannot be taken as evidence for the absence of a refuge. At least three effects could invalidate such reasoning, but these can only be addressed with further studies:

1. Geometrids are probably much faster dispersers than, for example, termites (Gathorne-Hardy, 2002; however, no quantitative dispersal data for tropical geometrids exist). Consequently, any Pleistocene effect on community structure may have diluted over the last 12,000 years. With a broader taxonomic database, future studies could test whether poorly-dispersing taxa are consistently more supportive of the refugial hypothesis than fast dispersers.

2. Our central Bornean sampling sites were close to the margin of a purported Pleistocene rainforest refuge (Fig. 1). Given the uncertainty in climatic models and associated ideas on vegetational change (Cannon et al., 2009), one cannot be sure that the sites were not actually inside the refugium. More data from sites in the south and south-west of the island are necessary for a thorough evaluation, yet they are not easily attainable due to logistical constraints.

3. Statistical comparisons were weakened by the low number of "non-refugial" sites (3, compared to 30 within the hypothetical refugium). However, such survey data from Borneo in general, and from Kalimantan in particular, are not easy to attain (hence the overall paucity of community-wide data available for such studies). Restricting the number of refugial sites to those from the north-east (i.e., Malaysian state Sabah) led to almost identical results as all data.

What can be concluded from this study, with all the above caveats, is a warning that refugial effects are not, in the assumed spatial extent, strong enough to be visible in our data. Considering only evidence from studies showing refugial effects could lead to false certainty on the reality of

refugia, reminiscent of the history of the refugial hypothesis in the Amazon (which many consider wrong by now; cf. Kircher, 2011, p. 74).

Our data on local diversity indicated no difference between north-eastern and central Borneo (with and without controlling for elevation), contrary to the commonly-held belief of higher diversity in Sabah. Diversity assessments are always scale-dependent, so higher landscape heterogeneity (e.g., topography) may lead to different conclusions on the level of regional species lists (no data available yet). However, our results are also consistent with the idea that differences in sampling effort, rather than real diversity differences, are responsible for the impression of a north-eastern peak of diversity. Species distribution modelling of hawkmoths (family Sphingidae) also indicated no north-south differences in local diversity across Borneo (at 5 km grain size; L. Ballesteros-Mejia, IJ Kitching & J Beck, unpublished) yet there are too few southern samples to evaluate the reliability of this assessment.

Ballesteros-Mejia et al. (2013) and Yang et al. (2013) have recently pointed out the importance of spatial sampling bias, explaining ca. 90% of species richness data variability across large regions. Indonesian Borneo is less accessible to scientific exploration than Malaysia due to logistics. Administrative challenges (visas and permits), in particular, affect biogeographic research projects that require a large spatial spread of sampling sites (and hence, many permits; Renner et al., 2012). Resulting biases in data have to be considered when analysing available data.

Understanding the impact of past climatic changes in today's species distributions is not only relevant for a general understanding of the region's biogeography, but also for formulating scientifically sound conservation policies. In the absence of detailed distributional data, model extrapolations are often used to identify regions where a particular species occurs (Wilting et al., 2010) or where biodiversity is particularly high (Slik et al, 2009; Beck et al., 2011; Ballesteros-Mejia et al., 2013). Such models assume, by design, no historical effects – a crucial assumption that requires thorough investigation.

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APPENDICES

Appendix 1. Full geometrid data from Camp Foyle (Murung Raya District, Kalimantan Tengah: Sungai Mohot, a tributary of S. Joloi; see "Murung Raya Expedition 2011", www.heartofborneo.org); latitude −0.092, longitude 113.488, elevation 200 m a.s.l.). 3 samping sites were located <1 km north of the Camp/River: MRE2, small forest gap at camp; MRE3, 50 m height on emergent tree, >15 m above remaining canopy; MRE4, dense forest understory. Nomenclature and identifications are based on Holloway (1986–2012). See Methods for treatment of genera *Thallasodes* and *Pelagodes*. Two further specimens from MRE4 could only be identified to genus (*Achrosis*, *Synegia*) due to poor specimen conditions; these were ignored for analysis.

Species	MRE2	MRE3	MRE4	Species	MRE2	MRE3	MRE4
Abaciscus paucisignata	0	0	1	*Hypochrosis binexata*	16	26	22
Achrosis calcicola	0	0	3	*Hypochrosis cryptopyrrhata*	13	1	13
Acolutha pictaria	1	0	1	*Hypochrosis pyrrhophaeata*	16	4	6
Actenochroma muscicoloraria	1	0	0	*Hypochrosis sternaria*	2	0	2
Agathia largita	0	0	1	*Hypomecis costaria*	45	0	28
Antitrygodes divisaria	1	0	0	*Hypomecis lioptilaria*	12	0	12
Antitrygodes vicina	1	0	1	*Hypomecis separata*	12	0	5
Astygisa circularia	0	0	1	*Hypomecis sommereri*	3	0	0
Astygisa metaspila	0	0	1	*Hypomecis subdetractaria*	33	0	22
Astygisa vexillaria	0	0	1	*Hypomecis tetragonata*	12	0	8
Berta annulifera	3	0	0	*Hyposidra aquilaria*	3	0	2
Berta chrysolineata	1	0	0	*Hyposidra infixaria*	2	0	10
Biston pustulata	0	0	1	*Hyposidra picaria*	1	0	0
Bracca maculosa	0	0	2	*Hyposidra talaca*	0	2	8
Celenna centraria	11	0	5	*Idaea craspedota*	2	1	4
Chorodna complicataria	1	0	0	*Iulotrichia decursaria*	2	0	4
Chrysocraspeda ozophanes	0	0	1	*Lomographa luciferata*	1	0	0
Cleora biclavata	0	0	2	*Lomographa sectinota*	0	0	1
Cleora contiguata	0	0	4	*Luxiaria acutaria*	0	0	2
Cleora cucullata	0	0	4	*Luxiaria submonstrata*	1	0	5
Cleora onycha	0	0	3	*Luxiaria subrasata*	0	0	1
Cleora propulsaria	0	0	1	*Metallolophia vitticosta*	0	0	1
Cleora pupillata	1	0	0	*Microcalicha delika*	1	0	0
Cleora tenebrata	0	0	3	*Microcalicha minima*	1	0	0
Comibaena cassidara	0	0	1	*Naxa kerangatis*	3	0	0
Comostola dyakaria	0	0	1	*Omiza lycoraria*	2	2	19
Comostolodes albicatena	0	0	1	*Ophthalmitis viridior*	1	0	0
Comostolodes dialitha	1	0	0	*Organopoda acerbata*	0	0	1
Coremecis incursaria	5	0	4	*Ornithospila avicularia*	12	0	9
Coremecis maculata	0	0	2	*Ornithospila bipunctata*	2	0	0
Craspedosis arycandata	0	0	1	*Ornithospila submonstrans*	0	0	2
Cusiala boarmoides (ssp. *acutijuxta*)	0	0	1	*Ornithospila succincta*	1	0	0
Diplurodes 14218	0	0	2	*Paramaxates polygrapharia*	0	0	2
Diplurodes decursaria	0	1	1	*Parasynegia fortilineata*	0	0	1
Diplurodes kerangatis	0	1	1	*Pelagodes* sp.	0	2	3
Diplurodes sugillata	1	1	0	*Peratophyga hypsidesma*	1	0	0
Dooabia puncticostata	0	0	2	*Peratophyga venetia*	2	0	1
Ectropidia altiprimata	2	0	0	*Peratophyga xanthyala*	0	1	1
Ectropidia exprimata	0	0	1	*Perixera decretarioides*	0	0	1
Ectropidia quasilepidaria	1	1	1	*Petelia medardaria*	0	0	1
Ectropis bhurmitra	1	0	0	*Petelia paroobathra*	0	0	1
Eois memorata	0	0	1	*Petelia tuhana*	0	0	1
Eumelea florinata	1	0	0	*Pingasa rubicunda*	1	1	4
Fascellina castanea	0	0	1	*Pingasa ruginaria*	1	1	9
Fascellina meligerys	1	0	0	*Pingasa tapungkanana*	1	0	4
Fascellina punctata	1	0	1	*Plutodes argentilauta*	0	0	1
Godonela avitusaria	1	0	1	*Plutodes cyclaria*	0	0	2
Godonela translineata	0	0	2	*Plutodes malaysiana*	0	1	1
Heterolocha pyreniata	0	0	1				

Species	MRE2	MRE3	MRE4
Pomasia galastis	1	0	0
Pomasia reticulata	0	0	1
Problepsis plenorbis	1	0	0
Protuliocnemis partita	0	0	1
Pseudopolynesia amplificata	0	0	1
Racotis inconclusa	1	0	2
Scopula insolata	0	0	1
Spaniocentra megaspilaria	0	0	1
Sundagrapha lepidata	0	0	1

Species	MRE2	MRE3	MRE4
Sysstema pauxilloides	2	0	0
Tanaorhinus rafflesii	0	0	3
Tasta reflexoides	0	1	0
Thalassodes sp.	0	0	9
Yashmakia loxozyga	0	0	1
Zeheba lucidata	0	1	1
Zythos obliterata	0	0	2
Zythos strigata	1	0	0
Zythos turbata	4	0	0

Appendix 2. Among other Macrolepidoptera, we recorded one male *Drapetodes interlineata* Warren (family Drepanidae; *det.* from picture by J. D. Holloway) at Camp Foyle (site MRE2). This is the first record of the species for Borneo; other specimens are known from Java and the Malay Peninsula [Photograph by: J. Beck].

Appendix 3. Table of all 33 sampling sites, their location, and hypothesized refugial status.

Site	Refugial status	Lat [°]	Long. [°]	Elev.[m]	Forest stratum	Year	Region	Sampling details in:
MRE2	not refug.	−0.092	113.488	200	underst.	2011	Murung Raya	[NA]
MRE3	"	−0.092	113.488	200	canopy	2011	"	[NA]
MRE4	"	−0.092	113.488	200	underst.	2011	"	[NA]
W10	refug.	4.965	117.792	220	underst.	2003	Danum Valley	Beck et al. (2006) J. Zool.. Soc. Wallacea 2: 44-53.
W10_N5	"	4.97	117.792	220	underst.	2003	"	"
W10_S5	"	4.96	117.792	220	underst.	2003	"	"
W15	"	4.965	117.787	220	underst.	2003	"	"
W15_N5	"	4.97	117.787	220	underst.	2003	"	"
W15_S5	"	4.96	117.787	220	underst.	2003	"	"
W5	"	4.965	117.797	220	underst.	2003	"	"
W5_S5	"	4.96	117.797	220	underst.	2003	"	"
DV1_I	"	4.965	117.796	220	canopy	2001	"	[NA]
DV2	"	4.962	117.858	263	canopy	2001	"	[NA]
DER_A	"	5.32	117.55	80	underst.	1998	Deramakot	Chey (2002) Malayan Nat. J. 56: 23-41.
Ser1c	"	6.22	116.7	430	canopy	1997	Serinsim, Kinabalu	Beck et al. (2002) J. Trop. Ecol. 18: 33-51.
Ser1g	"	6.22	116.7	430	underst.	1997	"	"
Ser2c	"	6.26	116.7	270	canopy	1997	"	"
Ser2g	"	6.26	116.7	270	underst.	1997	"	"
LE_J	refug. (uncertain)	1.55	112.25	150	underst.	1998	Lanjak-Entimau	Chey (2000) Malayan Nat. J. 54: 305-318.
LE_A	"	1.48	112.11	325	underst.	1998	"	"
LE_L	"	1.481	112.1	310	underst.	1998	"	"
LE_D	"	1.55	112.251	150	underst.	1998	"	"
LE_F	"	1.48	112.1	300	underst.	1998	"	"
MUL23	"	4.135	114.893	250	canopy	1978	Gn. Mulu	Holloway (1984) Saraw. Mus. J. 30(51), Spec.Iss 2:148-191.
MUL21	"	4.149	114.891	130	underst.	1978	"	"
MUL20	"	4.1489	114.891	150	underst.	1978	"	"
MUL19	"	4.1423	114.892	100	underst.	1978	"	"
MUL18	"	4.0573	114.826	50	canopy	1978	"	"
MUL17	"	4.1372	114.894	100	canopy	1978	"	"
MUL16	"	4.0591	114.830	150	canopy	1978	"	"
MUL11	"	4.0593	114.865	150	underst.	1978	"	"
MUL8	"	4.0601	114.829	90	underst.	1978	"	"
MUL7	"	4.0593	114.865	150	canopy	1978	"	"