The macroecology of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae)

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PREFACE

> (...) "After my long experience, my numerous failures, and my one success, I feel sure that if any party of naturalists ever make a yacht-voyage to explore the Malayan Archipelago or any tropical region, making entomology one of their chief pursuits, it would well repay them to carry a small-framed [white-washed] veranda, or a veranda-shaped tent of white canvas, to set up in every favourable situation, as a means of making a collection of nocturnal Lepidoptera" (...)
>
> ALFRED RUSSEL WALLACE
>
> (The Malay Achipelago, 1869)

Following Wallace's advice, a wealth of data on the distribution and abundance of moth species has been collected in Southeast-Asia and the 'Malay Archipelago' during the last 135 years. The objective of my research work is to use this information in conjunction with my own field sampling, in order to analyse some ecological properties of moth assemblages in the light of modern theories on biodiversity and community ecology.

My aim of analysing species' distribution, abundance and the relationship between them made it necessary to also pay attention to patterns of biodiversity and biogeography, which are direct results from these variables, as well as to some methodological issues. Furthermore, additional parameters such as larval host plants and body sizes were treated as they might influence one or the other variable.

Each topic is presented as a chapter or sub-chapter with an own introduction, methods description and discussion. It can be read without referring to the other chapters and allows faster editing of each chapter's results for publication in scientific journals. An introduction describes the 'macroscopic perspective' (Maurer 1999) on community ecology, the research taxon and region and some general methodological issues. A general discussion and synthesis can be found at the end of this work, and summaries in English, German, Malay and Indonesian (which is the most widely understood language of Southeast-Asia) are given.

At the time of submission of this thesis, Chapter 2 is accepted for publication in the *Journal of Research on the Lepidoptera 39*:

- Beck & Linsenmair, *Feasibility of light-trapping in community research of moths: Attraction radius of light, completeness of samples, nightly flight times and seasonality of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae)*.

Chapter 3.1 was in shortened form submitted to *Biodiversity and Conservation*:

- Beck & Linsenmair, *Effects of habitat disturbance can be subtle yet significant: biodiversity of hawkmoth-assemblages (Lepidoptera: Sphingidae) in Southeast-Asia*.

Associated with the thesis is an Internet website (Beck & Kitching 2004) in which additional information (graphs, pictures & maps) can be found.

CHAPTER 1

GENERAL INTRODUCTION

1.1 The concept of Iarge-scaled ecological research

`Macroecology' is a new word (Brown & Maurer 1989) for an old research agenda that can be traced back at least to the works of A.J. Lottka in the 1920's (Maurer 1999). Macroecological approaches already had a flourishing period in the 1960's and 70's (for example with the works of F.W. Preston and R.M. May) before the interest in the analysis of large-scale ecological patterns was recently revived (Brown 1999). As elaborately pointed out by B.A. Maurer (1999), the 'macroscopic perspective' an community ecology is an addition to smaller-scaled research, addressing the problem that local studies an single or few species may succeed in describing and explaining an investigated situation, but often do not retrieve general patterns that can be transferred to other taxa, times or sites (Maurer 1999, 2000, see also Boero et al. 2004). Rather, a broader scale of analysis - in taxonomy, time and space - is advocated (see Blackburn & Gaston 2002), hoping it may uncover patterns or `laws' (Colyvan & Ginzburg 2003) that focus less an the properties of single specimens or species, but an emergent properties of community Organisation - just as thermodynamic theory describes the properties of gasses in terms of pressure, temperature and volume without paying much attention to the movements of single molecules (Lottka 1925, cited in Maurer 1999, but see Hanski 1999; see also Jorgensen & Fath 2004). Some prominent 'macroecological' patterns might exemplify this intention: The species richness of an area grows with the size of that area (the 'species-area relationship', Scheiner 2003, Rosenzweig 1995) and with the energy that is available for biological processes (e.g. Bonn et al. 2004, Rajaniemi 2003). Species are more often small than big, and small species occur in higher population densities (e.g. Rosenzweig 1995, Maurer 1999, Blackburn et al. 1992). Furthermore, there are more rare than common species (e.g. Robinson 1998), and local rarity or commonness appears to be related to the geographical distribution of species (e.g. Gaston 1996a) - the latter relationship will be a major topic in this work (chapter 6).

With the documentation, linkage and causal understanding of such patterns, macroecology might be able to connect the various fields of ecological and evolutionary science, such as biodiversity research, population ecology and biogeography (Maurer 2000, Blackburn & Gaston 2001). Advances in some of these fields are particularly important in tropical ecosystems, where scientific understanding of the systems is low in comparison to temperate systems, yet biological diversity and complexity are high and anthropogenic landscape conversion and the accompanying destruction of ecosystems are rapid (Linsenmair 1997, Groombridge 1992, Wilson 1992, WBGW 1999, see Jepson et al. 2001, Matthews 2002 for data from Indonesia), thus calling for applicable counter-strategies. Understanding biodiversity changes and its interplay with human activities is already now a prerequisite for successful conservation and management efforts (e.g. Moritz et al. 2001, Hector et al. 2001, Reid 1998, Hanski 2004, Jennings & Blanchard 2004, Gaston et al. 2000). Being able to manipulate such changes in a directed way is an important goal for the future (see e.g. Janzen 1998, 1999).

Two consequences of the `macroecological' research agenda have strong impacts an its methodologies and interpretations: *1) Large-scaled investigation can usually not be experimental* because of the ecosystem-wide extent of most investigated patterns. In some cases it might be possible to use smaller-scaled model systems that can be manipulated (e.g. Holt et al. 2004, Warren & Gaston 1997, Lawton 1998, 2000), but ultimately effects have to be documented an 'life-size' systems to be credible. As a consequence, deductive methods have to be applied, whereby the common patterns in nature as well as exceptions to them are documented and used for hypothesis generation (including quantitative models), which are then tested an further 'descriptive' data (see also Wilson 2003, Bell 2003, Boero et al. 2004). Descriptive data may contain biases and parameter collinearities, which often make it necessary to apply various data transformations, corrections or multivariate approaches (e.g. Southwood & Henderson 2000, Legendre & Legendre 1998). *2) Macroecological thinking is inherently neutral* - individual species identities and their properties are usually not of much concern (Maurer 1999), although explicit ecological neutrality of species (i.e. all specimens, regardless of species identity, have equal fitness) is assumed only in some models (e.g. Bell 2001, 2003, Hubbell 2001, McGill & Collins 2003, Ulrich 2004). Neutrality is an increasingly employed assumption in ecological models that leads to considerable simplifications, yet often retrieves patters which seem to be dose to empirical data (e.g. Hubbell 2001, but see McGill 2003a, b, Purves & Pacala in press). The neutrality assumption remains problematic because it is *known* that species are not neutral (i.e., species are adapted to certain habitats and niches, Begon et al. 1996) - but the differences between species might have no significant impact an the investigated patterns (Hubbell 2001). However, in apparent contradiction to this, good knowledge of the individual species characteristics is an essential prerequisite of all macroecological research, be it for data acquisition (e.g. choice of investigated taxa, successful field work), analysis (e.g. sensible exclusion of particular species) or interpretation (e.g. *post hoc* hypotheses, outlier Interpretation, etc.). Particularly if data are not sampled in own field work but retrieved from published sources it might be necessary to consult taxonomists and experienced naturalists to consider potential problems in data (which might not be explicitly stated in published data) or to interpret results properly. Furthermore, differences in patterns between various taxa, guilds, life histories or regions (e.g. Hillebrand 2001) might give important clues an the causal mechanisms behind the patterns.

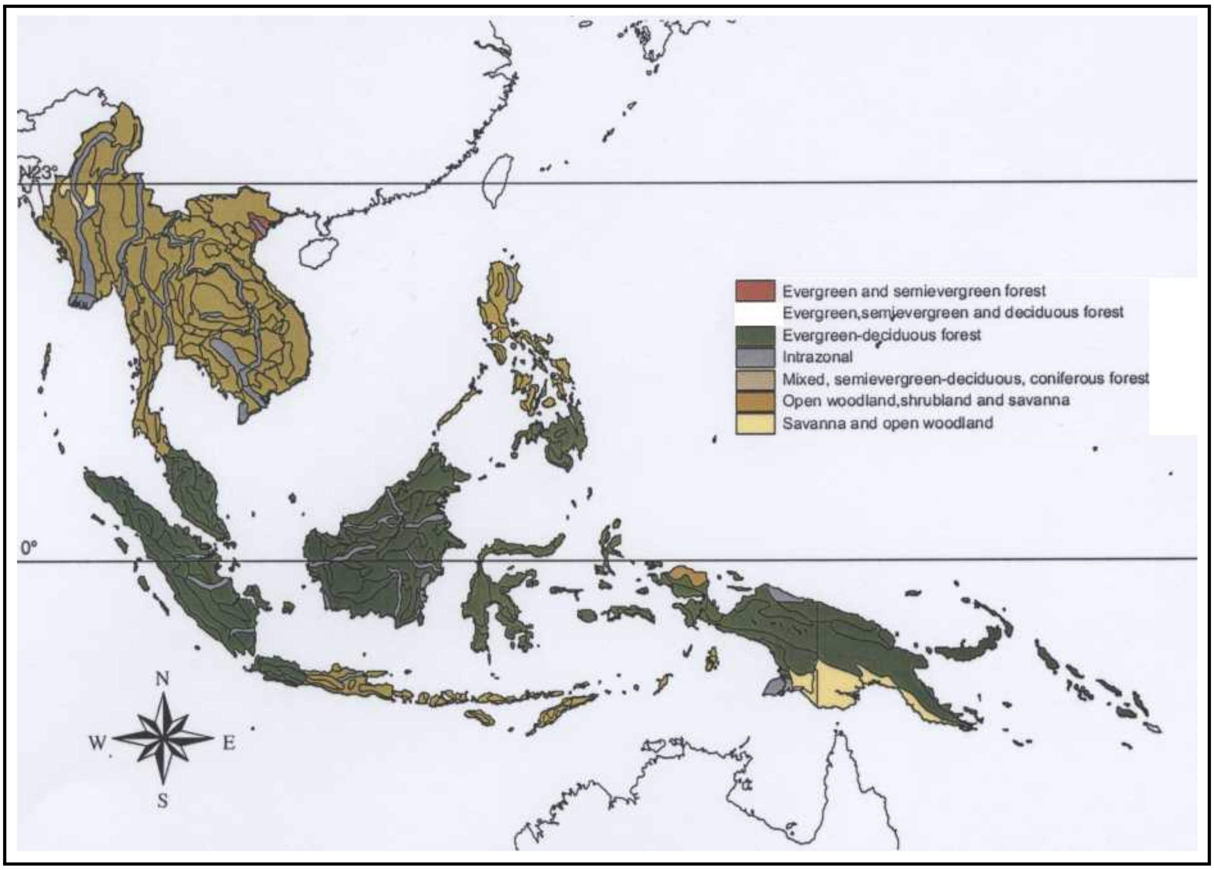
Advances in the search for causalities will probably mostly be made by explicit, quantitative models (Maurer 1999), which make precise and multiple predictions that can be validated against empirical data (McGill 2003b). The study presented here contains too many data insufficiencies to explicitly test complex model predictions - there are better data Sets (e.g. the British & North American bird counts) for such purposes. However, it may add valuable data for a detailed and comprehensive documentation of patterns for a taxonomic group and a geographic region that so far has been rarely used for macroecological investigation.

1.2 Study region and study taxon

a) 'Southeast-Asia' and the Malesian archipelago

The biologically and geographically diverse region lying between tropical oriental Asia and Australia has been the site of fruitful specimen collection and biological investigation since A. R. Wallace's travels in "The Malay Archipelago" (1869). The region covered by this study comprises the countries Burma/Myanmar, Thailand, Laos, Vietnam, Cambodia, Malaysia, Singapore, Brunei, the Philippines, Indonesia, East Timor, Papua New Guinea, the Solomon Islands and the Andaman and Nicobar Islands of India (see map). However, some biogeographically related regions are excluded, such as Guam, Palau, southern China (e.g. Hainan Island and Guangdong) and northern Australia (e.g. Arnhemland and the Cape York Peninsula), whereas data from Taiwan is included only in some analyses.

With its almost entirely tropical location, Southeast-Asia houses a very rich and varying assemblage of habitats and biotas, caused by large altitudinal gradients that range from lowlands to alpine glaciers (e.g. above 5000 metres in New Guinea; see Wong & Phillips 1996 for a detailed ecological coverage of the altitudinal zonation of Mt. Kinabalu in Northeast-Borneo) as well as the very heterogeneous geographic structure of Malesia (the archipelago between Peninsular Malaysia and the Solomon Islands) with its great differences in the size, isolation, geology and geographical history of various islands. Evergreen,



The map shows extent and major landscape zones of Southeast-Asia as defined in this study. It ranges from Burma (Myanmar) in the north (ca. 28°30'N) to Rennel Island (Solomons) in the south (ca. 11 °30' S), and from the Andaman Islands in the west (ca. 92°30' E) to the Santa Cruz group (Solomons) in the east (ca. 167° E) [latitudinal extent: ca. 4.500 km; longitudinal extent: ca. 8.200 km, area size ca. 4,22 Mill. km^2].

Dipterocarpaceae-dominated rainforest is the dominant natural Vegetation in the non-seasonal, equatorial lowland regions (e.g. Whitmore 1990, Cranbrook & Edwards 1994), while more seasonal regions are covered with various types of seasonal forests (e.g. Monk et al. 1997). A comprehensive source an information about the ecology and natural history of the region is the `Ecology of Indonesia'-series (Hong Kong: Periplus Editions, Ltd.).

The complex biogeography and geology of Southeast-Asia and the Malesian archipelago (Hall & Holloway 1998, Whitmore 1981, 1987) is mirrored by diverse cultures and societies, and a great variation in population densities, logistic conditions and political situations - from tribal societies to ultra-modern cities (e.g. Turner et al. 2000, Rowthom et al. 2001). The region undergoes massive landscape conversions since ca. 50 years, mainly caused by commercial logging and large-scaled Land clearing for plantations, which will have long-term ecological impacts and create considerable cultural changes as well as social tensions (e.g. Sodhi et al. 2004, Jepson et al. 2001, Monk et al. 1997, Matthews 2002, Manser 1996).

b) Lepidoptera: Sphingidae

General and detailed information about hawkmoth systematics, morphology, ecology and natural history can be found in the recent works of Kitching & Cadiou (2000), Lemaire & Minet (1998), Holloway et al. (2001), Common (1990), or online in Pittaway (1997). Here, only information which might be significant for the research topics in this study is reviewed.

The Lepidoptera family Sphingidae is systematically placed among the Bombicoidea, the Same superfamily as the silk moths (Holloway et al. 2001). While Sphingidae are among the taxonomically relatively well-known non-vertebrate groups, some features of their phylogeny and classification still remain unclear - for example, the Smerinthini (see table 1) are paraphyletic and are just tentatively classified as tribus (Kitching & Cadiou 2000). Kitching & Cadiou (2000) present a classification in subfamilies, tribes, subtribes as well as tentative phylogenetic groupings of the Sphingidae genera, which is applied (in an updated version, I.J. Kitching pers. com.) as a provisional phylogenetic working hypothesis in this study - but many of these relationships are far from confirmed and some are completely unresolved.

Subfamily	**Tribus**
Smerinthinae	Smerinthini
	Ambulycini
	Sphingulini
Sphinginae	Sphingini
	Acherintiini
	Cocytüni*)
Macroglossinae	Macroglossini
	Dilophonotini
	Philampelini*)

Table 1: Higher classification within the family Sphingidae (Kitching & Cadiou 2000). *) Taxa do not occur in Southeast-Asia.

Worldwide over 1300 species are currently known, whereas new species keep being discovered at a rate of ca. 15 species per year (I.J. Kitching pers. com.; five new species were found in Southeast-Asia during this study's timeframe of four years). Within the boundaries of Southeast-Asia (as defined above) 375 described species are known (Beck & Kitching 2004).

Sphingidae share the four-stage life-history of holometabolous insects (see e.g. Pittaway 1997 for details) with solitary, large folivorous caterpillars and very mobile, fast flying adults. With massive bodies and wingspans up to 20 centimetres (Kitching & Cadiou 2000, see e.g. chapter 5.2), Sphingidae are among the largest Lepidoptera. Despite an overall quite small range of body sizes among the family there are differences in average body size and -shape between the subfamilies - Macroglossinae have shorter wings and a larger thorax in relation to the wing size than other subfamilies (chapter 5.2), a fact that could influence flight abilities and dispersal of the taxa.

Most adult Sphingidae feed an flower nectar which presumably allows them to imbibe energy in the form of carbohydrates, but probably only few proteins or amino acids. Adult search for amino acids or protein, which occurs in other taxa an flowers (e.g. Alm et al. 1990, Erhardt & Baker 1990, Erhardt 1991, Dunlap-Pianka et al. 1979, see also Blüthgen & Fiedler 2004a, b and references therein) and elsewhere (Beck et al. 1999, Bänziger 1975, 1979, 1980, 1986), has not been studied in detail in the Sphingidae, but there are indications of nitrogen-related 'mud-puddling' in various species (Bänziger 1988, Büttiker 1973). Furthermore, some unusual adult feeding habits occur, such as stealing honey from bee's nests (in *Acherontia sp.)* and tear-drinking an large mammals (Bänziger 1988). Very little is known about the specificity of flower visits of adult hawkmoths, but it has been observed that Sphingidae apparently remember the location of rich nectar sources and visit them again (Janzen 1984, Pittaway 1997). Many Smerinthinae, particularly of the tribus Smerinthini, are not feeding as adults (as may be concluded from a missing or reduced proboscis; it is to date not really clear if this is a plesiomorphic character within the Sphingidae, I.J. Kitching pers. com.), while the adult feeding habits and their ecological consequences (see below) in the tribus Ambulycini (see table 1) requires further attention. Ambulycini have a reduced, yet probably functional proboscis, an which flower pollen were found in six species of the genera *Ambulyx* and *Amplypterus* from Borneo (J. Beck & N. Blüthgen, *unpubl.).* Ambulycini appear intermediate between the non-feeding Smerinthini and the feeding adults of other subfamilies, with a larval biology similar to the former group, but traits of Sphinginae- or Macroglossinae adult behaviour (see also chapter 7 for discussion).

Adult diet has an influence an life-span and egg production in Lepidoptera (e.g. Karlson 1994, Hill 1989, Hainsworth et al. 1991). The lack of adult feeding in some groups is influencing their life-history with probably far-reaching ecological and behavioural consequences (e.g. Tammaru & Haukioja 1996, see also Janzen 1984 for a thorough discussion): Non-feeding adults have to produce all eggs from larval resources *(capital breeders),* while their adult life is presumably relatively short. Feeding adults, an the other hand, can use adult resources for egg production and body maintenance *(income breeders),* and thus have a potential for a longer adult life-span (see also the discussion of *semelparous vs. iteroparous* organisms in Begon et al. 1996).

Parasitoids from a wide range of taxa are known to attack hawkmoth eggs and caterpillars of the Western Palaearctic region (see Pittaway 1997 for details), including nematode worms, Hymenoptera (Trichogrammatidae, Ichneumonidae, Braconidae) and Diptera (Tachinidae), which can lead to a mortality of up to 80 percent in some investigated caterpillar populations (see Pittaway 1997 for references). Known predators of larva and adults are invertebrates (ants, social wasps, beetles, spiders) as well as vertebrates (mice, shrews, birds, bats, cats; Pittaway 1997, Giardini 1993). Sphingidae rely mostly an crypsis as a means of predator escape, but eyespots (as snake-mimicry) in caterpillars and startling pink and yellow hindwings in adults occur in some taxa (Kitching & Cadiou 2000). Sequestration of toxic secondary plant compounds for protection against predators is apparently rare (Kitching &

Cadiou 2000), although such cases occur, sometimes in combination with suspected aposematic coloration. Mimicry of large Hymenoptera occurs in some day-active taxa. Some hawkmoths produce sound when disturbed, which might startle potential predators (e.g. in *Acherontia sp.),* while it could be related to yet unexplored mating behaviour in other cases (e.g. *Psilogramma sp.).* Night-activity of caterpillars and adults as well as flight speed and agility are probably also main predator escape strategies (Evans & Schmidt 1990). Furthermore, many species have strong tibial spurs which they use effectively for defence if captured. Parasitism and predation can be interacting with the structure of Lepidoptera communities (Stireman & Singer 2003, Barbosa & Caldas 2004, Scheirs & DeBruyn 2002, Lill et al. 2002, Gilbert & Smiley 1978), but too little is known about their respective effect an Southeast-Asian hawkmoth species to explicitly consider such effects in this study.

Hawkmoths were chosen as focal study taxon in this project for a number of reasons: (1) They are a suitable `model group' for ecological investigations (e.g. Sutton & Collins 1991, Pearson 1994) due to the availability of a comparatively large amount of background information (taxonomy, host plants, distribution; e.g. Kitching & Cadiou 2000, Pittaway & Kitching 2003, Pittaway 1997), which is matched for tropical invertebrates only by butterflies (e.g. Fiedler 1998). Although no complete phylogeny exists for the family, the taxonomy is relatively stable and reliable, a prerequisite for the compilation of multi-source data as well as for phylogenetic controls in comparative analyses (e.g. Harvey & Pagel 1991). This wealth of information (particularly an distribution and food plants) is not the least because hawkmoths are, presumably due to their large body size, a favourite taxon for Lepidoptera enthusiasts and hobby collectors, and have been so for more than a century. Some common North American species *(Manduca* sp.) are also frequently used as `model species' in (eco-)physiological research (e.g. Kessler & Baldwin 2001), yet these results had only very limited impact an the topics that were studied here. (2) An investigation an hawkmoths makes a reasonable 'case study' as their general life history, with a folivorous caterpillar stage and a winged mating and dispersing stage, is probably typical of many other taxa of herbivorous insects, particularly of the Macrolepidoptera. Sphingidae are important pollinators (e.g. Haber & Frankie 1989, Kitching & Cadiou 2000) and some species have a potential to be agricultural pests (Moulds 1981, 1984, Kitching & Cadiou 2000 and references therein). Furthermore, caterpillars as weil as adults are even utilised for human nutrition in various regions (Kitching & Cadiou 2000 and references therein, I.J. Kitching pers. com, Chey V.K. pers. com), all of which gives them some economic importance. (3) Most hawkmoth species are attracted to artificial light sources, which are an efficient method of assessing biodiversity, relative abundance and faunal inventories of nocturnal Lepidoptera (e.g. Muirhead-Thompson 1991). Other methods of quantitatively inventorying insect assemblages (e.g. net-catches along transects for day-active butterflies) are probably more error-prone (i.e. biased towards conspicuous and slow species), and certainly much more work-intensive. (4) Hawkmoths are large and relatively species-poor even in Southeast-Asia if compared to mega-diverse groups such as the Lepidoptera families Geometridae (e.g. Scoble et al. 1995, Gaston et al. 1995) or Noctuidae. This makes them relatively easy to identify - an important factor in the study of tropical insects, where identification can make a significant proportion of the total workload (Basset et al. 2004, Brehm 2000) and species-level determination may sometimes not be possible (e.g. Wagner 1996, 1999, Oliver & Beattie 1994). On the other hand, local and regional species richness is high enough to attain sufficient sample sizes for comparative analyses. Most specimens could be reliably identified alive in the field or from digital photographs with the help from a specialist (Dr. I.J. Kitching, Natural History Museum, London). This has not only the ethical advantage that not many specimens had to be killed (but see Holloway et al. 2001, McKenna et al. 2001 for the relatively small impact of scientific collecting an natural moth populations), but also reduced the necessity to export specimens for further determination, which is a sensitive issue in many developing countries due to fears of unilateral bioprospecting (Castree 2003, Makhubu 1998).

Species nomenclature in this study mostly follows the Checklist of Kitching & Cadiou (2000), together with some more recent species descriptions. However, other recently described species were not considered valid and therefore ignored even though they are not (yet) formally rejected. Similarly, in a few cases revised species boundaries were adopted, which are based an preliminary studies of which publication is pending. Four undescribed specimens and one subspecies which will soon be raised to species status (I.J. Kitching pers. com.) were also included into analyses although formal descriptions are pending.

1.3 Retrieving and processing information for macroecological research

Macroecological analyses have frequently been conducted an already existing, comprehensive data sets which List parameters like body size, local abundance estimates and geographical distributions of taxa (e.g. Johnson 1998b, Blackburn et al. 2004, Gaston & Blackburn 1996). With the exception of a few thoroughly listed data Sets (e.g. BirdLife International/European Bird Census 2000), such information often exists in the form of atlases for taxa of public (i.e. birds, mammals & butterflies) or commercial interest (e.g. timber trees). The main reason for the bias against the study of various relationships in tropical insects (e.g. Gaston 1996a) is because such data are mostly not available (see also Blackburn & Gaston 1998), at least not in a ready-to-use form. However, much of the needed information might actually be there, only scattered over various collections or publications and in strikingly different forms, depending an why the data was originally sampled (see also O'Connell et al. 2004). The increasing use of the Internet is a chance to retrieve such treasures and make them widely accessible for analysis.

Here an example of retrieving distribution information for Southeast-Asian hawkmoths is outlined, focussing an major methodological issues rather than an results (which can be found in other chapters).

Collaborations

The necessary data for comprehensive ringe analyses can never be sampled by a single person (or research group) in a `normal' 3-6 year research project. Thus, besides scanning the relevant literature (which often involves non-peer-reviewed, local magazines as well as various internet resources), collaboration with institutional and private collections is the most efficient way to access data. In this project, collaboration with Dr. Jan J. Kitching gave access to data from the British Museum of Natural History (London) and the Carnegie Museum (Pittsburgh), covering extensive collection material of more than 150 years as well as a data bank of published distribution records. While there is certainly an element of luck in finding such a fruitful collaboration, large data sets of collected specimens of various taxa are increasingly becoming available online from the world's major museums (see e.g. Graham et al. 2004, McCarter et al. 2001). Networking led to further data sources like other museums and private collectors (see acknowledgements). Collaborations as well as unilateral data 'presents' are probably most likely when people are working in completely different fields - 1 did not meet a single taxonomist or hobby collector who was not willing to share his data with me for ecological analyses.

Taxonomic competence

Although various alternatives to species-based analyses have been proposed for macroecology, conservation and biodiversity research (e.g. Petchey & Gaston 2002, Williams & Gaston 1994, Williams et al. 1994, Riddle & Hafner 1999, Oliver & Beattie 1993), analyses of species are the main focus of most studies as they form a natural entity that can mostly be named and identified an the basis of morphological traits (Kelt & Brown 2001), and are thus also applicable to historical collection material. Compiling multi-source distribution data requires profound taxonomic competence to ensure that species identities from various data Sets actually refer to the Same species (Graham et al. 2004). Revisions, splitting of subspecies or regional populations into 'good species', synonymies and name changes lead to a lot of confusion if data from several decades or even centuries are compiled, which can only be sorted out reliably and with reasonable effort by someone who is already well familiarised with the taxonomy of the respective group (see e.g. Isaac et al. 2004). Thus, this is yet another call for the importance of taxonomic expertise (see also Wheeler 2004), which is also indispensable for proper applications of phylogenetic controls (e.g. Harvey & Pagel 1991) in comparative evolutionary and macroecological studies.

Processing geographic injbrmation

Over 34,500 records for the worldwide distribution of the hawkmoths that occur in Southeast-Asia, New Guinea and the Solomon Islands were compiled (one 'record' referring to the information that a species was found at a certain place in a certain year, although it might involve many specimens). Although ca. six percent of records included specific information an the latitude and longitude of sampling sites (usually recent records with GPS-data), the geographic Position of most records had to be found with the help of the Internet, online gazetteers and various atlases, both modern and old. By this rather tedious procedure it was possible to assign latitude and longitude to ca. 90 percent of the records with an accuracy of at least 1 degree latitude and longitude. In many cases it was relatively straightforward to find the sites, but a certain degree of detective and sometimes educated guesswork was required to find places that had changed name, spelling or that are not mapped at all. Reconstructing collector's travelling routes (considering likely means of transport) often yielded the necessary clues as to where a site was probably situated. Ca. four percent of the records were not sufficiently detailed to assign them an a 1 degree grid (site information such as Southeast China' or 'Japan') and were tentatively assigned to the most likely 1°-square, based an collection time, infrastructure and the 'popularity' of regions for collectors. A Small number of records (ca. 0,1 percent) raised considerable doubt regarding their credibility for various reasons. Based an the likelihood of misidentifications in some species or the risk of mislabelling or misspelling in large collections, they were ignored for estimating species' ranges - although future sampling might, of course, prove them to be correct.

Records were entered into a Geographic Information System (GIS: *ArcView 3.2),* which allowed displaying them by species, subspecies, record accuracy, altitude or year of sampling (if known). As a base map the world map of *ArcView* seemed sufficiently detailed, although some small islands in the Philippine/Moluccan region and the South Pacific were missing (these were hand-digitized from various naval maps and inserted into the world map where necessary). A number of freely available, GIS-compatible habitat maps were used to 'underlay' the species records in order to determine patterns of distribution. Altitudinal relief, Vegetation zones, precipitation and minimum winter temperature often matched the outer limit of records, and a number of apparently important parameters for moth distributions could be identified (see also chapter 4.2, Beck & Kitching 2004 for details).

Uneven sampling effort in different regions can disturb this straightforward procedure: Whereas an unrecorded species in well-sampled northern Thailand or northeast Borneo probably indicates its absence from that region, it is most unlikely to do so in undersampled Laos, Burma/Myanmar or southern (Indonesian) Borneo. Furthermore, certain species are more likely to be overlooked (or misidentified) than others. Taking all these factors into consideration, the best possible estimate of each species range was digitized. Area sizes and other measures of distribution can easily be calculated from the range estimates (e.g. Hooge et al. 1999) and recorded and estimated species checklists for regions (countries, islands, grid-squares) can be extracted from overlaid range maps.

Similar approaches to estimating Lepidoptera species ranges have previously been used in computerised (e.g. Cowley et al. 2000) and non-computerised (Hausmann 2000, pers. com.) form. The use of GIS does not only make it easier and more precise to find distribution patterns by overlapping the records with maps of potentially important habitat parameters, but it also allows to use the resulting range maps for further computer-aided analysis. However, no explicit computer model was used here to estimate ranges (see also Holloway et al. 2003 for a `semi-computerised' habitat model). Computer models have been successfully used for range estimates an a smaller geographic scale (e.g. Raxworthy et al. 2003, Ray et al. 2002, Iverson & Prasad 1998) and would be desirable for their fast applicability to a large number of species. However, the analysis of presence-only data which is typical for museum data (Graham et al. 2004) is still problematic for statistical habitat models (e.g. Zaniewski et al. 2002, Cowley et al. 2000). A computerised habitat model (M. Wegmann & J. Beck, preliminary trails using Diva-GIS: Hijmans et al. 2001, 2004) was felt to perform inferior in tackling the biases in data quality (e.g. Graham et al. 2004, Soberön et al. 2000, Fagan & Kareiva 1997). Despite the apparent 'subjectivity' of the approach that was chosen here, a 'brain-model' (as opposed to a computer model) is probably still more precise due to an easier consideration of species differences, be it ecological requirements, if known, or recording constraints. However, rapid methodological advances make computerised GIS models a very promising future Option (e.g. Segurado & Araujo 2004, Engler et al. 2004, Rushton et al. 2004, Lehmann et al. 2003, Mackey & Lindenmayer 2001).

Online publication

The Internet is not only a suitable forum for finding and exchanging data, but also to present processed data. Besides the difficulty of finding a chance to publish range maps for 380 species, online publications have the advantage that they can be easily updated when new information becomes available (or errors and misinterpretations are recognised), and may allow the user to download processed data directly in a suitable format. Particularly taxonomical work will increasingly rely an online presentations in the future, and attempts of unifying such attempts (e.g. by creating reviewed taxonomy portals) are discussed already (see e.g. Graham et al. 2004).

To present the processed information an hawkmoth ranges, a website ('The Sphingidae of Southeast-Asia', Beck & Kitching 2004: http://www.sphingidae-sea.biozentrum.uni-wuerzburg.de ; see also colour plates (box 1. 1) at the end of this chapter) was created. Besides general information an the aims and methods of the project it lists all species which were recognised as valid in this study, although without the claim of a taxonomic revision or checklist. Pictures of almost all species as well as range maps (showing original records and estimated ranges) are presented and reported as well as estimated checklists for 114 Malesian islands can be found. This information will be updated whenever substantial changes in taxonomy (e.g. new species descriptions, revisions) or new, extending distribution records become available. The website links geographically to similar sites an the Western and Eastern Palaearctic region (Pittaway 1997, Pittaway & Kitching 2003).

Conclusion

Hawkmoths are certainly an exceptionally well-known group of insects, both with regard to their taxonomy as well as their distribution (see also chapter 1.2). Still, for a number of other tropical insect taxa it might also be possible to retrieve and process data in a similar fashion as was outlined here for Sphingidae, which would enable comparisons to the results an biodiversity, biogeography and macroecology that are presented in this thesis. Particularly other macrolepidoptera groups, social insects and maybe the more conspicuous beetle families (e.g. Cerambycidae, Cicindelidae) are probably relatively well-covered in scientific and/or hobby collections. However, as exemplified above, a widespread, networking collaboration of researchers and institutions is needed to compile data comprehensively and taxonomic expertise must ensure adequate processing of data. GIS-based display and spatial modelling have great potential to retrieve sound estimates from scattered presence-only data, particularly if computerised modelling procedures become available (and are properly tested) for 'batch-processing' of range-estimates of many species at a time. Publication of results as well as processed data in digital form would enable fast `colTections' in the light of new data or new taxonomical developments.

The Sphingidae of Southeast-Asia

(incl. New Guinea, Bismarck & Solomon Islands) Back to start page, species list

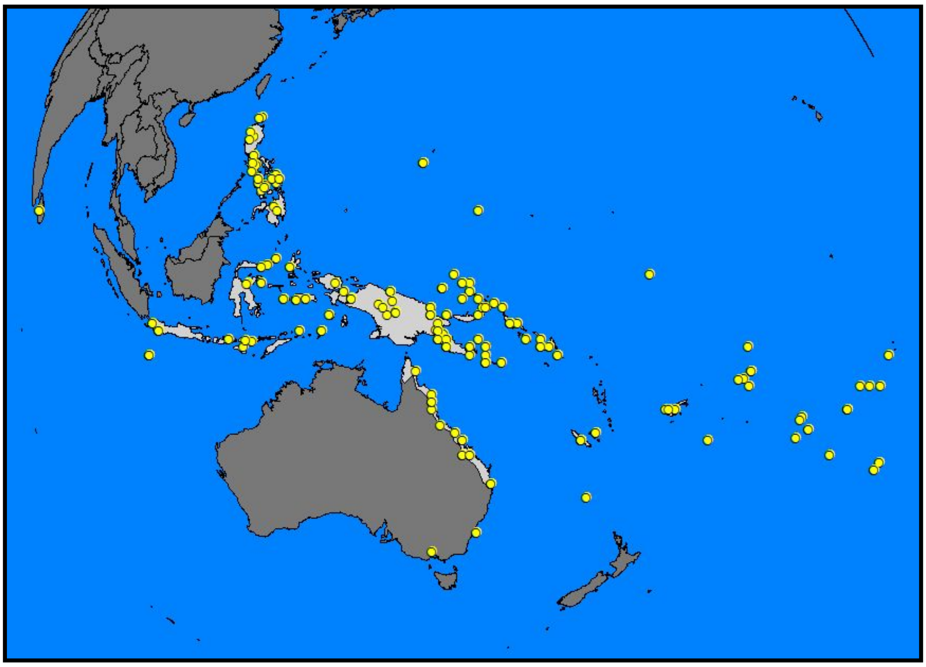
by Jan Beck & Ian J. Kitching

Gnathothlibus eras (Boisduval, 1832)

Taxonomy

Preliminary analysis of adult morphology suggests that the western populations (*G. erotus* sensu stricto) and the eastern populations (*G. eras*) of *Gnathothlibus erotus* sensu lato may not be conspecific. This provisional assessment is followed here pending further more detailed study.

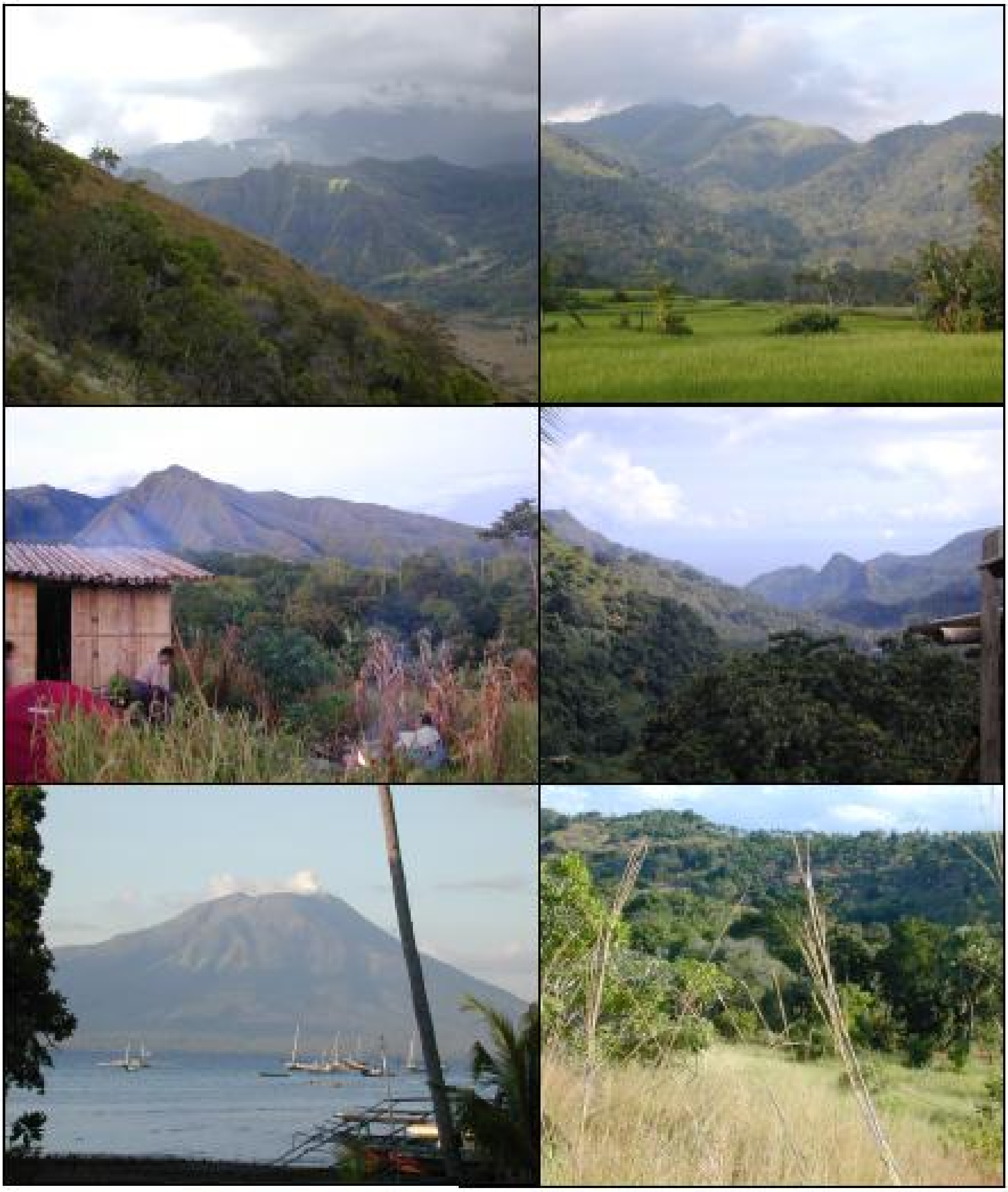
Distribution



Two individuals are reported from Sri Lanka: a female which could be either *G. eras* or *G. erotus*, and a male that is confirmed as *G. eras*, but is considered a stray or vagrant. Likewise, the two records from southern Australia (Victoria, New South Wales - Cronulla) are considered vagrants.

Box 1.1: An example of the species information as it is presented in the **Internet webpage of Beck & Kitching (2004)** is provided. Pictures and font have been edited to fit the printed page format.

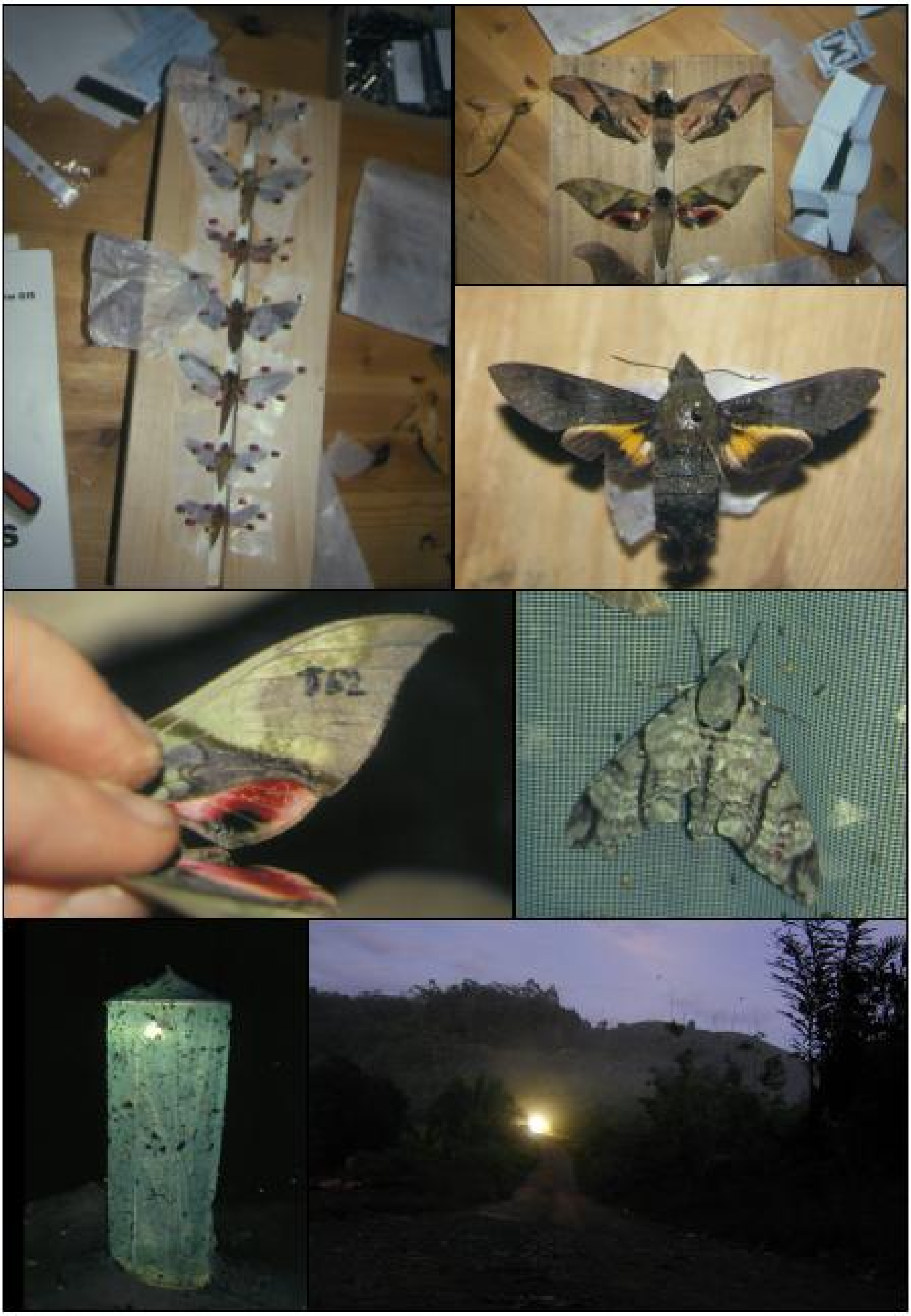
Landscapes in Borneo: Lowland forest at Danum Valley (upper), Mt. Silam near Lahad Datu (mid-upper, left), Kinabatangan River (mid-upper, right), Crocker Range (mid-lower, left), local agriculture near Poring village (mid-lower, right), heath-forest near Bario (lower left), logging road to Long Pasia (lower righ).



Landscapes on the Lesser Sunda Islands: Slopes of Mt. Inerie (upper left), rice fields and slopes of Mt. Kelimutu (upper right), sampling sites in central Flores (middle), smoking vulcano on Lembata island (lower left), dry forest and savannah on Adonara island (lower right).

Landscapes in New Guinea: Lowland rainforest in the Cyclops mountains (upper left), swamp forest near Timika (upper right), montane agricultural areas around the Baliem valley (ca. 2000 metres a.s.l., middle), shore of Lake Sentani (lower left), north coast at Dabra (lower right).

Digital images of hawkmoths are a suitable way of determining specimens in local collections and in the field without collecting, exporting, and often even without killing them: *Ambulyx tattina* (Borneo, upper left), *Callambulyx amanda* (Borneo, upper right), *Marumba timora* (Flores, middle left), *M. juvencus* (Borneo, middle right), *Hippotion boerhaviae* (New Guinea, in natural day-time resting position, lower left), *H. brennus* (New Guinea, lower right).



Field methods: Mounting, spreading and drying of specimens (upper), individual marking with waterproof pen (middle), 125 Watt Mercury-Vapour 'light-tower' at close range and from 100 metres distance (lower).

CHAPTER 2

FEASIBILITY OF LIGHT-TRAPPING IN COMMUNITY RESEARCH OF MOTHS

Abstract

Experimental data and quantitative samples of Sphingid assemblages from tropical Southeast-Asia were analysed to investigate methodologically relevant topics of light-trapping.

Mark-Release-Recapture experiments revealed differences in the attraction radius of a light source between lepidopteran families, but no such differences could be found between 18 species within the family Sphingidae. Attraction radii (for 50 percent return rate within 5 minutes) were generally below 30 metres, which confirms results from previously published studies.

Specimen arrival of Sphingidae at a light source was symmetrically distributed around midnight, and species differed significantly in median arrival time. No evolutionary hypothesis for such flight time differences could be confirmed from data.

At an appropriately chosen sample site (avoiding dense undergrowth), all-night sampling with a 125 Watt MV-lamp yields more than ¾ of the expected species richness of Sphingidae in an average of 5-6 sample nights. Seasonality and temporal changes of local assemblages can probably be neglected for comparisons of samples from largely non-seasonal regions like Borneo if data stem from a relatively short study time of a few years.

In conclusion, (1) there are no indications that light trapping 'draws' specimens from far-away habitats to the sampling site. (2) No proof was found that species within the family Sphingidae are differentially drawn to light, which would lead to biases if light-trapping data was used as a measure of relative abundance in the habitat. (3) Such biases, on the other hand, probably exist between taxonomically or morphologically more divers taxa (e.g. for different families) and must be considered for a proper interpretation of light-trapping data. (4) Light-trapping is an effective means of assessing the species composition and relative abundances of Sphingid assemblages in Southeast-Asia, but sampling has to be carried out all night in order to maximise catch size and avoid biases due to different nightly flight times of species.

Introduction

The use of artificial light sources is by far the most commonly employed technique to attract night-active Lepidoptera for the study of taxonomy, biogeography and biodiversity (e.g. Holloway et al. 2001, Intachat & Woiwod 1999). While neither the physiological mechanism (Spencer et al. 1997, Sotthibandhu & Baker 1979, Hsiao 1973, Bowden 1984) nor the evolutionary significance (e.g. Holloway 1967) of this well-known attraction is known to a satisfying degree, this technique offers a number of advantages over alternative methods such as torchlight-transects (Birkinshaw & Thomas 1999), baiting with fruits, red wine (Süssenbach & Fielder 1999, 2000), cheese or shrimp paste (S. Benedick & J. Hill, pers. com.), malaise traps (e.g. Butler et al. 1999), suction traps, rotary traps or other methods of passively sampling the air space (see Southwood & Henderson 2000):

Light trapping yields a large number of specimens with a minimum of effort (Holloway et al. 2001, Fiedler & Schulze 2004). This is particularly true for mechanical light-traps (see Southwood & Henderson 2000 for an overview of designs), which do not even require the presence of the researcher during trapping. However, some groups of Lepidoptera such as Sphingidae, which are the main subject of this study, have a tendency not to enter such traps in large numbers, but to settle on the outside and in the perimeter of the light source. A comparison between data from mechanical light-traps (Nasir Abd. Majid pers. com.) and hand-sampling at light (own data) showed a ca. 30-fold higher yield for the latter method in lowland Borneo (see also Brehm 2002, Axmacher & Fiedler 2004). Thus, for the rest of this work, the term 'light trapping' refers to attracting moths with light, but sample them by hand or net. Light can be assumed to sample the community more 'neutrally' than traps baited with food or pheromones, where specialisations are more likely to occur. Last but not least, light trapping allows sampling and killing most specimens relatively undamaged, an important requirement for precise species identification, which is not met by many 'passive' sampling techniques such as malaise or rotary traps.

On the other side, a number of objections to light trapping have been put forward and lepidopterologists regularly face sceptic criticism by journal reviewers when publishing light-trapping research. The unresolved question of why moths actually come to light (see above for references) does not help to the scientific credibility of the method. The main arguments against light trapping in community ecology (see also Schulze & Fiedler 2003a, Brehm 2002 for a more detailed discussion), as well as common responses to these arguments, are:

1) Light traps sample communities selectively rather than randomly. Besides measuring activity rather than relative abundance (see e.g. Wolda 1992, Simon & Linsenmair 2001), not all species are attracted to light to the same extent (Bowden 1982, Butler et al. 1999). Some species of hawkmoth are rarely or not at all attracted to light, but can be caught in numbers by other methods (e.g. Butler et al. 1999, Kitching & Cadiou 2000). Some species seem to be attracted only in parts of their range (e.g. the Sphingid *Daphnis nerii* comes to light in Africa, but not in Asia; I.J. Kitching, pers. com.). Females are generally rarer in light catches of Lepidoptera than males (see e.g. Brehm 2002 for data), which might reflect differences in activity as well as in attraction to light between the sexes. Thus, it might be suspected that relative abundances of species at light are as well distorted by differential attraction to light

and different levels of flight activity. While these potential problems are undeniable, their actual effect on the results of studies on the community ecology of moths remains to be quantified. Light trapping has often been proven to produce readily interpretable and ecologically meaningful results in studies on the biodiversity of Lepidoptera (e.g. Holloway 1976, Schulze & Fiedler 2003a, Fiedler & Schulze 2004). Furthermore, the constraints of light trapping are shared with any other comparable sampling method (Schulze & Fiedler 2003a, Southwood & Henderson 2000).

2) The effective attraction radius of light sources might be so large that moths are drawn from other habitats to a sampling site. Measurements of the attraction radii of light produced distances of three to 250 metres (depending on study method and species; Muirhead-Thompson 1991, Bowden 1982), but attraction radii are probably smaller than 30 metres in most situations for 'normal' light sources in entomological research (Butler & Kondo 1991, Muirhead-Thompson 1991). Furthermore, studies on the stratification of moth communities in the forest produced clear community differences between strata at height differences of 20-30 metres (e.g. Beck et al. 2002, Schulze & Fiedler 2003a, Beck & Schulze 2003, using 15 Watt blacklight sources). Thus, while it is a common point of criticism, there is actually little indication of an effect of 'drawing' specimens to light from far away habitats.

3) The abundance of specimens at light is influenced by weather, moon and vegetation. While the effect of vegetation density around a sample site might be overestimated (Schulze & Fiedler 2003a), effects of moonlight and weather (temperature, rain, fog, wind) have been clearly documented and discussed (e.g. Persson 1976, Muirhead-Thompson 1991, Holloway et al. 2001, Intachat et al. 2001, Yela & Holyoak 1997, McGeachie 1989, Brehm 2002). Generally, warm, moist and moonless nights produce highest specimen counts, as has been already noted by R.A. Wallace (1869). Thus, abundances at light can never be used as reliable indicators of absolute population sizes in a region, but must be adequately 'converted' into figures which are comparable across samples with regard to the initial question of a study (Southwood & Henderson 2000).

Different light sources (power, wavelength) might also influence sample size and species composition (though this is mainly anecdotal; see Brehm 2002), as does the time of the night during which a trap is operated (e.g. Schulze 2000 found a steady decline in Pyraloidae specimens during the first 3 hours of the night in samples from tropical Borneo).

In an attempt to add new quantitative data to this discussion, two sets of questions were experimentally investigated in Sphingidae and other lepidopteran families in Southeast-Asia:

1) What distances of light attraction can be found under 'real life' research conditions in a tropical habitat? This is particularly interesting for the Sphingidae - very large and extremely fast- and far-flying moths, which might thus be expected to exceed known figures of light attraction radii.

2) Is there evidence for differences in the attraction radius a) between Lepidoptera families with largely differing size, body shape and flight ability, and b) between species of the family Sphingidae? Such differences would be a clear indication that relative abundances of moths

at light might present a distorted picture of real abundances, even if species which do not come to light at all (e.g. largely day-active taxa such as *Macroglossum*) were not considered.

Furthermore, sampling data were analysed to assess answers to the following general problems of sampling tropical insect populations:

3) What percentage of a local tropical community of hawkmoths can be sampled in a short-term light trapping program? While this question is not particular to light trapping but to any time-constrained ecological study, it is an important background figure to interpret light trapping results.

4) How does the nightly trapping time influence specimen numbers and species composition of samples? It has been suggested (e.g. Kitching & Cadiou 2000, Diehl 1982) that certain species can only be successfully caught at certain times of the night, but so far no quantitative data for whole local assemblages were available.

5) How does seasonality or other temporal changes in the Sphingid assemblages of wet-tropical Borneo affect the credibility of results from short-time sampling of local assemblages? While it is often inferred from the climatological stability of tropical habitats that seasonal changes in communities are minute compared to temperate regions, significant effects of weather and season (mostly defined by rainfall) on insect populations have been shown (e.g. Intachat et al. 2001, Novotny & Basset 1998, Wolda 1978, 1988, Wolda & Flowers 1985, Tanaka & Tanaka 1982, Kato et al. 1995, Smythe 1985). Such effects are often ignored in ecological studies in the tropics, as time and logistic constraints do usually not allow for year-round, long-term sampling.

Methods

a) Field methods

Attraction radius experiments

During two field seasons in 2001/2002 and 2003, four suitable sampling sites in north-eastern Borneo (Sabah, Malaysia; see table 2.1 for details) were chosen for release experiments. Site characteristics that influenced this choice were a high yield of Sphingid specimens (known from previous sampling), overall favourable logistic conditions and the existence of a straight stretch of logging road of at least 120 metres length. A generator-powered mercury-vapour bulb (125 Watt) was placed inside a white, cylindrical gaze-'tower' with a height of approximately 1,7 metres from the ground. Sampling was carried out in the time of reduced moonlight from a week before new moon until a week after new moon in order to maximise catch size. Nightly sampling was carried out from ca. ½ hour after sunset until ½ hour before sunrise, except if logistic problems made this routine impossible.

All arriving Sphingidae were hand-sampled from the light or nearby vegetation (<ca. 3 metres radius), measured (forewing-length), determined (Holloway 1987a, D'Abrera 1986, Kitching & Cadiou 2000) and marked individually with a waterproof pen on the forewing. Rare species were either killed and taken for closer taxonomical examination or stored inside the gaze cylinder for release at dawn, while common species (≥14 specimens, see table 2.2)

were used for experiments and released from randomly chosen distances along a logging road (distances in 5 metre steps, from 5 up to 120 metres, at one site up to 130 metres). After preliminary trials, moth were transported to the release distance inside a plastic jar (500 ml) immediately after handling and were released by turning the jar upside-down, thus without giving the moths an initial flight direction. While this procedure carries the risk of un-directional, panicking flight rather than providing an ideal situation for deliberately choosing a flight direction, it avoided the effect that moths which were kept for a prolonged period after catching to 'cool down' after handling often refused to fly at all when released and sat on the same spot for hours. Catch time, release time and -distance and re-catch time of all specimens at the light were noted. Each specimen was released only once, after re-catch it was stored inside the gaze cylinder for release at dawn. Re-catches of marked specimens in following nights were not considered at all, but their occurrence at a rate of ca. 5 percent indicates that the marking does not harm the moths (see also Beck & Schulze 2000, Beck et al. 1999). One species, *Dapnusa ocellaris*, was excluded from analysis as it was frequently observed trying to escape on foot rather than by flight after handling (see discussion).

For a comparison between lepidopteran families, several morphospecies from non-Sphingid groups were chosen for their commonness and easy identification under field-conditions (Holloway 1986, 1993a, 1996a). However, in some cases these morphospecies might have contained several species of a genus, which were impossible to separate alive and in the field (see table 2.3). These considerably smaller and more delicate moths had to be caught, marked and handled with special diligence. Specimens which were accidentally injured were excluded from experiments.

Site	Nights	Released moths	Latitude	Longitude	Elevation a.s.l. [m]	Habitat	Region
CRO1	9	285	5,44°	116,08°	1170	Ridge with road & planted banana fields, overlooking PF valley & mountains	Crocker Range Park
DV3	5	34	4,96°	117,86°	220	selectively logged (1988), opening along road	Danum Valley
DV4	6	134	4,97°	117,84°	340	selectively logged (1988/89), along road overlooking valley	Danum Valley
POR8	14	1.127	6,03°	116,77°	350	Local agricultural area near village	Poring Hot Springs

Table 2.1 lists details for all sampling sites in north-eastern Borneo at which release experiments were conducted. Note that latitude and longitude are given in metric format. Additional sampling sites which were re-sampled and used for assessments of seasonality are both on canopy platforms in primary dipterocarp forests at Danum Valley (DV1) and at Poring Hot Springs in Kinabalu Park (POR1). See appendix I for site acronyms.

Family	Species	Individuals	Comments
Sphingidae	*Acherontia lachesis* [Fabricius]	42	
	Acosmeryx anceus [Stoll]	16	
	Acosmeryx shervillii [Boisduval]	70	
	Ambulyx canescens [Walker]	37	
	Ambulyx moorei [Moore]	38	
	Ambulyx pryeri [Distant]	49	
	Ambulyx substrigilis [Westwood]	20	
	Amplypterus panopus [Cramer]	19	
	Cechenena helops [Walker]	40	
	Daphnis hypothous [Cramer]	211	
	Marumba juvencus [Rothschild & Jordan]	14	
	Megacorma obliqua [Walker]	20	
	Psilogramma menephron [Cramer]	147	
	Theretra clotho [Drury]	112	
	Theretra latreillii [W. S. Macleay]	49	
	Theretra nessus [Drury]	184	
	Theretra rhesus [Boisduval]	260	
	Theretra silhetensis [Walker]	18	
Geometridae (Ennom.)	*Biston* 3sp. [Leach]	31	*B. inouei* [Holloway], *pustulata* [Warren] or *insularis* [Warren]
	Celerena signata [Warren]	22	
	Dalima subflavata [Felder & Rogenhofer]	36	
	Pingasa chlora [Stoll]	44	
Geometridae (Geomn.)	*Thalassodes*-complex (24sp.)	34	Genera *Thalassodes*, *Pelagodes* or *Orothalassodes*
Noctuidae (Aganainae)	*Asota* 4sp. [Walker]	67	*A. plana* [Walker], *albiformis* [Swinhoe], *heliconia* [Linneaus] or *egens* [Walker]
Σ Sphingidae		**1.346**	
Σ Geometridae		**167**	
Σ Noctuidae		**67**	

Table 2.2 lists all 24 species (1.580 individuals) that were included in the release experiments. 18 species belong to the family Sphingidae, five species to the Geometridae and one to the Noctuidae. Some of the non-Sphingid species could not be reliably determined under field conditions and might refer to any of the species listed in the right column.

Data for completeness of samples, flight time and 'seasonality' comparisons

Data for an assessment of the faunal completeness of short-time, high-intensity light trapping stem from an extensive sampling program in Southeast-Asia, which was carried out from early 2001 to early 2004. Except of the four sites at which release experiments were conducted (see above), all sampling schedules were carried out independently of weather or moonlight conditions, so effects of these factors on abundance or flight time of moths should be randomly distributed. Generally, Sphingidae were hand-sampled (as described above) all nights for 3-9 consecutive nights in a block. Median nightly sampling time was 10,2 hours. Sites with samples of less than 20 specimens within three nights were generally ignored. For the purpose of assessing the completeness of the applied sampling procedure, data for 15 sites in north-eastern Borneo and one in Peninsular Malaysia were used. Sampling habitats ranged from primary forests through variously disturbed forest types to open, agricultural landscapes, from lowlands up to almost 1500 metres elevation, and were generally situated either in open areas or in the forest canopy (platforms or at cliffs or steep slopes) in order to maximise Sphingid catch (see Schulze & Fielder 1997). Four sites in Sabah (north-eastern Borneo) were re-sampled up to four times during the three years of field work (see table 2.1 & 2.5, minimum 6 months between re-samples). These re-samples were used to assess effects of temporal change, but were considered as independent samples for the purposes of an evaluation of sample completeness, which raises the sample size to 23 sampling sessions.

At 11 sites in Borneo and one in Peninsular Malaysia detailed arrival time of all specimens was measured (in 15 minute-steps, data of all sites were pooled for this analysis).

b) Methods of analysis

Return times of the experimentally released specimens ranged between a few seconds to more than eleven hours, while ca. 47 percent of released moths were not seen again at all during the night of release. Some specimens obviously did not directly return to the light, but flew around in the area and were later attracted to the light source again. As a consequence, the rule was applied that only returns within five minutes since release were counted as '*returns*' for analysis, while any later arrivals were considered as '*no-returns*'. From literature on flight speeds (up to 20 m/s, Gatter & Gatter 1990 and references therein), own speed measurements (100 meters in less than 20 seconds for several Sphingidae species) and observations it was concluded that all species should be able to reach the light in that time interval even if they take some time to start or orientate after release. Return rates per minute sink rapidly within the first few minutes and reach a bottom level after about eight minutes (when 50% of all returning moths have come back to the light). Return rates after this point fluctuate apparently randomly (on a level of 0-2 percent return rate per minute) and probably represent released specimens which did not return directly to the light, but flew around in the area and entered the attractive radius of the light again at some later time, as described above. Preliminary analyses suggested that analyses with a five-minute return criterion yields a higher statistical power than longer return times (i.e., 8 min., 15 min.). After that time directional movements towards the light can probably not be expected any more.

Besides standard statistical procedures, the following methods of analysis were employed:

Loglinear Model

A loglinear model was used to test for influential factors on the frequency of *returns* vs. *no-returns*. Release distances were grouped into six 20 metres-classes (5-20m, 25-40m, etc.), release distances >120m were not used for this analysis, as they were not available from all sites. A multi-dimensional contingency table, containing the frequencies of *returns* as well as those of suspected influential factors (e.g. release distance class, species identity, etc.), was constructed with all possible interactions between these factors, and then tested against the actual data (for a detailed description of loglinear models see e.g. StatSoft 2003).

Logistic Regression

As a second mode of analysing the release experiment data logistic regressions were used (Trexler & Travis 1993). While carrying the disadvantage that not all data sets can be fitted well by a logistic regression (predicting *return/no-return* better than random, see below), this method allows assessing attraction radii in metres rather than just comparing them.

The logistic equation (see e.g. Trexler & Travis 1993) was fitted to the *return/no-return* (1/0) data (original data in 5 metre intervals). Regression values can be interpreted as probability for return (StatSoft 2003). The point of 50 percent return probability (x_i = *turning point* of the log. regression for species i) is used as a measure of attraction radius. The variance of x_i is calculated from the variance of the regression parameters (b_0, b_1) as

$$\hat{\mathrm{var}}(\hat{x}_i) = (\hat{x}_i)^2 \cdot \left[\frac{\hat{\mathrm{var}}(\hat{b}_i^0)}{(\hat{b}_i^0)^2} + \frac{\hat{\mathrm{var}}(\hat{b}_i^1)}{(\hat{b}_i^1)^2} \right], i = 1,2$$

For graphic display, 95 percent confidence intervals were assessed as 1,96(SD(x_i)). For a more rigorous test of the hypothesis of a difference between two *turning points*, a *z*-test was performed:

$$z = \frac{\hat{x}_1 - \hat{x}_2}{\sqrt{\hat{\mathrm{var}}(\hat{x}_1) + \hat{\mathrm{var}}(\hat{x}_2)}}$$

If $-1{,}96 < z < 1{,}96$, the null hypothesis ('no difference') is accepted, otherwise it is rejected.

Both the loglinear models and the logistic regressions were calculated with the computer program *Statistica 6.1* (StatSoft 2003).

Estimating total species richness

From the distribution of species in discrete samples an estimate of the total species richness at a site can be assessed by several methods (see Chazdon et al. 1998, Colwell & Coddington 1994, Colwell 2000, Melo et al. 2003). Of these, the non-parametric *Chao1*-estimator has proven robust in pilot studies (Chazdon et al. 1998, Peterson & Slade 1998) and yielded realistic figures in studies on temperate moths (Beck & Schulze 2003, Süssenbach & Fiedler 1999), where the total species richness is much better known than in tropical regions. Assessments of the species diversity of habitats by *Chao1*-estimates are often congruent to those with well established methods like Fisher's α or Hurlbert's rarefaction curves (e.g. Beck et al. 2002, Schulze 2000). *Chao1*-estimates were calculated with the computer program *EstimateS 5.01* (Colwell 2000).

The sequential correction of Hochberg (1988) was applied to control for spurious significances due to multiple tests from the same data set, and all results which did not pass the criteria are noted in the text. However, it was not considered necessary to control analyses of different data sets, even if they overlap or are nested within another (see also Moran 2003).

Results

1a) Release experiments: Loglinear models

A sample size of 1.527 released moths was available for loglinear model analysis. The data structure was not suitable to include all interesting variables (return frequency, distance, species identity, family affiliation, experimental site) into one model. Therefore, certain variables were tested in separate models.

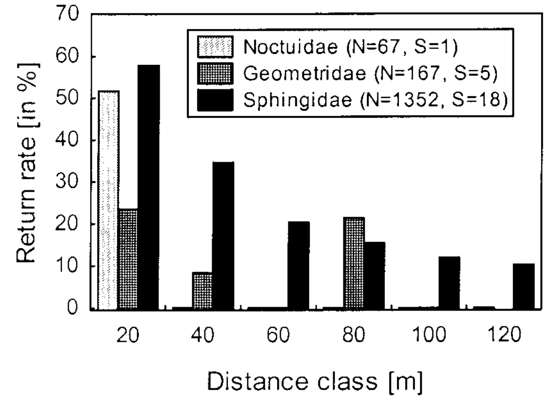


Figure 2.1 shows return rates within 5 minutes (in percent) of three Lepidopteran families from six release distance classes (note that 'Noctuidae' contains only the genus *Asota*, see table 2). Loglinear contingency table analysis (see box 1) indicates significant differences in return rates between the families.

The first model analysis (see box 2.1) suggests that the research site had no influence on return frequencies, so data from different sites were pooled for all further analyses. Family affiliation of specimens had a clear influence on return frequencies (see 2nd model in box 2.1, figure 2.1), while for 18 species within the family Sphingidae no

Box 2.1: Loglinear models.

Model 1: "Effects of research site" [site (4) x return (2) x release distance (6)] ***(N=1527)***

Model 1	χ^2 (Max. likel.)	df	p
Start model with 3 double-interactions	15,807	15	0,395
Best model (return-dist., site-dist. interactions)	18,715	18	0,410

Already the optimized model does not contain interactions of *research site* & *return frequency.*

Conclusion 1: No effect of site on return frequencies.

Model 2: "Effects of family" [*family* (3) x *return* (2) x *release distance* (6)] ***(N=1527)***

Model 2	χ^2 (Max. likel.)	df	p
Best model: 3fold- interaction fam. x return x dist	0	0	1
Exp. model 1: no 3-fold, but all 3 2-fold interactions	20,399	10	0,026
Exp. model 2: no 3-fold and no fam.-return interaction	54,360	12	<0,0001

The exclusion of the 3-fold interaction ("family influences distance-return interaction") leads to a significant difference between model predictions and real frequencies in data. Further exclusion of the family-return interaction brings another significant loss of prediction power of the model ($\chi^2_{df=2}$=34, p<0,0001).

Conclusion 2: Families have different return rates from different distances, i.e. different attraction radii. Beyond that, families differ in overall return rates (exp. model 1 *vs.* 2).

Model 3: "Effects of species" [species (18) x return (2) x release distance (6)]
(only Sphingidae, N=1352)

Model 3	χ^2 (Max. likel.)	df	p
Start model with 3 double-interactions	68,625	85	0,903
Best model (only return-dist interaction)	169,99	187	0,809
Exp. model without any interactions	298,73	192	<0,0001

Conclusion 3: No effect of species identity (within the Sphingidae) on return frequencies is evident; already the optimized model does not include species. The exp. model only proves the essentially expected effect of release distance on return rates – otherwise the experiments would have been senseless.

significant effect of species identity on return frequencies could be found (3rd model in box 2.1). All analyses show a significant effect of release distance on return frequencies. This was expected, the frequency of returns should decrease with diminishing light intensity at larger release distances.

Box 2.2: *Z*-tests for differences of logistic regression turning points (a) of families (b) of the most extreme species. Values in **bold** print indicate significant differences (z>1,96, p<0,05).

a)

z-value	**Sphingidae**	**Noctuidae**
Noctuidae	-0,664	
Geometridae	**2,173**	**2,418**

b)

z-value	*A. shervillii*	*T. latreillii*	*T. rhesus*	*Asota 4sp.*
T. latreillii	1,469			
T. rhesus	1,024	-0,956		
Asota 4sp.	0,908	-1,112	-0,307	
D. subflavata	1,790	-0,295	1,094	1,436

1b) Logistic regression

For the three families, as well as for 12 Sphingid species, logistic regression models could be constructed, while for 6 Sphingid species the models did not pass the χ^2-test of a better-than-random prediction of the data, which were consequently excluded from analysis. Figure 2.2 shows an example of a logistic regression for one species, figure 2.3 plots the attraction radii of the light (measured as the 50-percent 'turning points' of the regression) and their estimated confidence intervals.

On family level, 50% return rates vary between ca. 10-13 metres for Sphingidae and Noctuidae, and negative values for Geometridae. The differences between Geometridae and the other families are statistically significant at the p<0,05-level (see box 2.2), but do not pass the criteria of Hochberg (1988) for multiple tests from the same data set. The low value of Geometridae is mainly caused by very low return rates of *Pingasa* (5 returns of 44 releases) and particularly the small Geometrinae of the *Thallassodes*-group (5 of 34). The other Ennominae-species showed attraction radii comparable to that of Sphingidae or Noctuidae (data not shown).

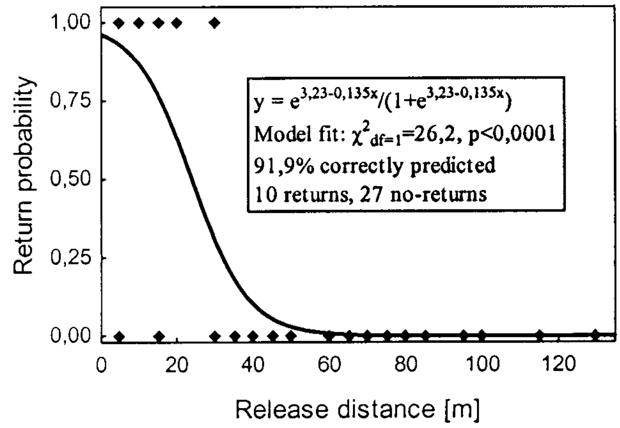


Figure 2.2 exemplarily shows a logistic regression fit to the binary data (*return/no-return*) of the Sphingid species *Ambulyx canescens* (N=37). Regression values (y-axis) range between 0 and 1 and can be interpreted as probability for 'return'. The 'attraction radius' (turning point of the regression = 50% return probability) is estimated at 23,9m for this species. Note that several data points may lie on the same position, which cannot be shown in the graph but influence the slope of the curve.

Turning points for Sphingid species vary between 26 metres and negative values (for species with very low return rates). Confidence intervals are large and indicate a high, unexplained variability in return behaviour. For two species no variance of parameters could be calculated due to the structure of the data matrix. Maximum confidence estimates range up to 60 metres, which is still a value in reasonable boundaries of the literature for attraction radii of light (see e.g. Muirhead-Thompson 1991). No significant differences between species could be found for the 10 species for which testing was possible.

Thus, the results obtained by logistic regression confirm the analyses with the loglinear models.

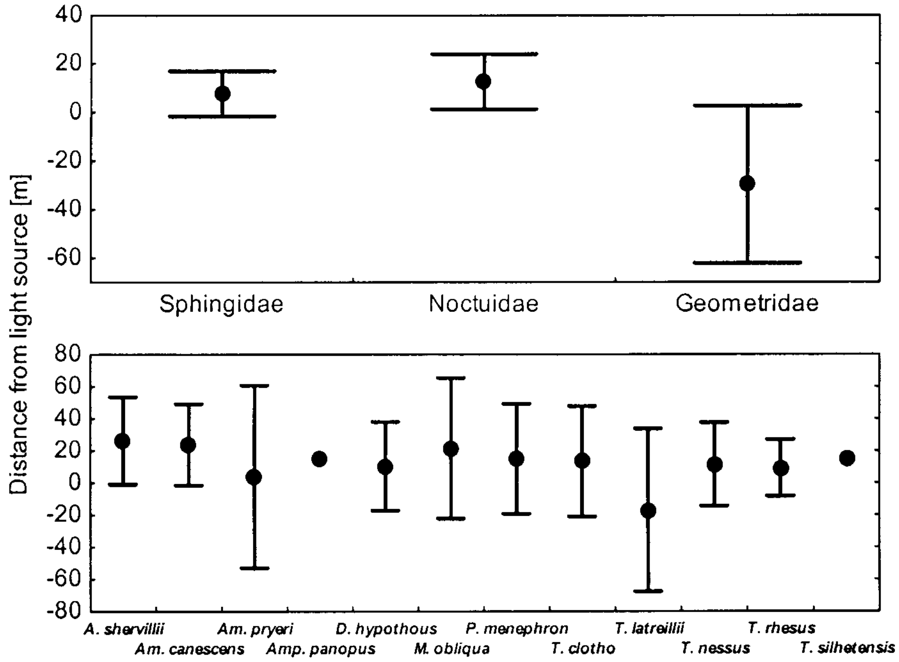


Figure 2.3 shows 'turning points' of logistic regressions, which indicate the distance of 50% return-probability (±1,96SD) after experimental release. Significant differences can be seen between families (upper graph), but not between species of the family Sphingidae (lower graph; see also box 2).

2) Completeness of samples

During an average of 5-6 nights per sampling session, an average of more than ¾ of the *Chao1*-expected 'true' species richness could be collected (see table 2.3 for details). Sampling success correlates with the number of sample nights as well as the number of sampled specimens (figure 2.4) but not with observed species richness or diversity (as Fisher's α).

	Mean ±SE	Median	Min.	Max.
N	**220,9 ±48,5**	116	25	847
S_{obs}	**22,1 ±1,5**		10	38
Nights	**5,5 ±0,3**		3	9
Chao1	**30,1 ±2,5**	28	14	68
$\%S_{obs}$	**75,9 ±3,2**		37,9	94,4
N/night	**35,9 ±6,5**	26,2	6,2	121

Table 2.3 presents the mean values of 23 sampling sessions for the number of individuals (N), species (S), sampling nights, as well as the *Chao1*-estimate of true species richness (Colwell 2000), the proportion (in percent) of observed/estimated species richness ($\%S_{obs}$), and the mean number of individuals per sampling night. The median is given where distributions deviate from normality (KS-test, $p<0{,}05$).

Measurements of sampling success based on other selected estimators of species richness (*ACE*, *Chao2*, *MMMeans*: see Colwell 2000) yield similar figures and correlate good with each other (Spearman rank correlations, N=23: R^2>0,463, p<0,001 for all except *Chao1:MMMeans*: R^2=0,261, p<0,013).

Comparison with other samples from the region

In table 2.4 the species richness (observed & expected) of the 23 standardized samples is compared to a combination of data from own samples, published literature (Chey 1994, 2002a, Holloway 1976, Tennent 1991, Zaidi & Chong 1995, Schulze 2000) and unpublished sources (Azmi Mahyudin, J.D. Holloway, pers. com.). These data vary in the use of different light types, sampling regimes and specimen numbers (local samples <20 specimens were not considered). Observed local species richness ranges up to 50 species (see figure 2.6: only samples >1000 specimens yielded over 40 species). Thus, the highest Chao1-estimate of 68 species (table 2.4) is still in a realistic range. The asymptotic slope of the data in figure 2.4 suggests that this may be the maximum local species richness that can be found by light-trapping in this region. Schulze et al. (2000) reported 59 night-active Sphingidae species from a compilation of data from several sampling sites within Kinabalu Park, Sabah. Higher records of local species richness can probably only be found from continental Southeast-Asia (e.g. 67 species from year-round sampling on a site in northern Vietnam, T. Larsen, pers. com.), where regional species richness is higher than in the

	N	Mean	SD	Min	Max
S_{obs} (own)	23	22,1	7,4	10	38
Chao1-est	23	30,1	12,1	14	68
All data S_{obs}	60	20,2	10,4	5	50

Table 2.4 shows the species richness (observed & estimated) of N local samples from Borneo and Peninsular Malaysia. See text for data sources of "all data".

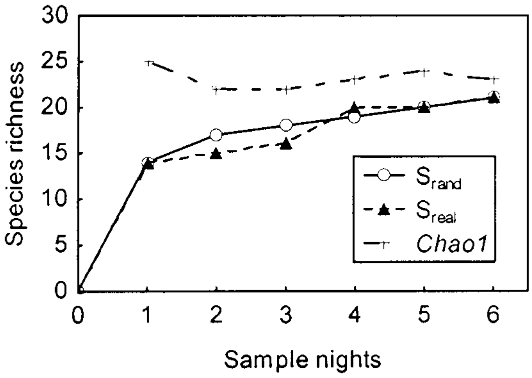


Figure 2.5 exemplarily shows species accumulation curves for a sampling site in Borneo (DV1-I): After 6 nights of sampling, 21 of 23 estimated species were caught (91,3% sampling success). S_{rand} is smoothened by a 100-fold randomization of the sample night order; *Chao1* is the estimate of total species richness at the respective number of (randomised) sampling nights. *MMMeans*, which fits an asymptotic curve to the species accumulation curve, yields an estimate of 22 species for this site. The total number of specimens is 437.

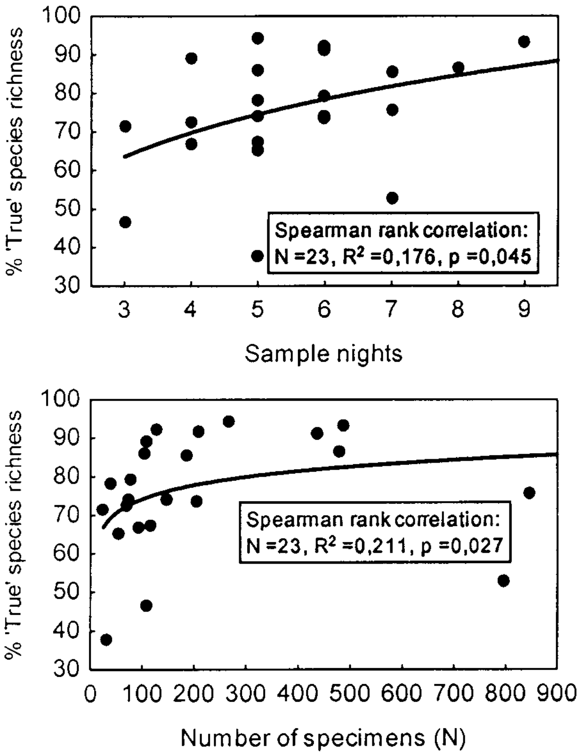


Figure 2.4 shows correlations between the number of sample nights (upper graph) and the number of sampled individuals (lower graph) and the percentage of sampled 'true' species richness (based on *Chao1*-estimates). A logarithmic regression was fitted for display, but none of the variables are normally or log-normally distributed (KS-tests, p<0,01). Each dot refers to a different sampling session, not to sub-samples from the same sampling session. An application of the Hochberg (1988)-correction for multiple tests from a data set makes the N-% *Species richness* correlation barely non-significant.

insular regions of Malesia (Beck & Kitching 2004, chapter 4.1).

3) Flight time during the night

Figure 2.7 shows the distribution of arrival times of 1.450 hawkmoths at 6 sample sites. Arrivals are clearly symmetrically distributed around midnight, with a steep rise in specimens in the third hour since sunset, and a decline after eleven hours. This is in marked contrast to smaller moths in Borneo or in temperate regions (e.g. Thomas 1996, Schulze 2000, own obs.), which considerably decline in numbers after 2-3 hours past sunset.

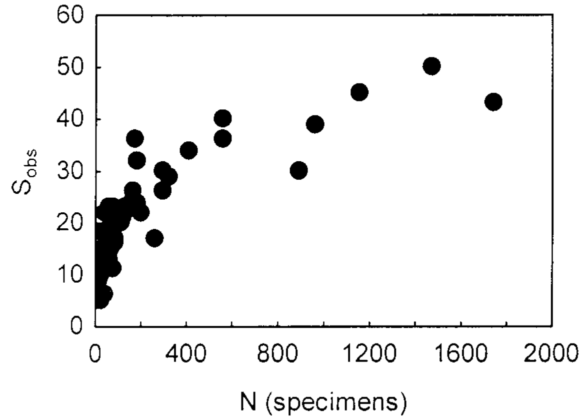


Figure 2.6 displays observed species richness of Sphingidae as a function of the number of sampled specimens for 60 local light-trapping samples from Borneo and Peninsular Malaysia (see text for data sources). The data are significantly correlated (N=60, Spearman's R^2=0,805, p<0,0001).

Of even greater methodological interest is figure 2.8, which shows that flight times clearly differ between different species. Median flight times also differ between Sphingid subfamilies, with Smerinthinae flying on average earliest in the night and Sphinginae latest (KW-Anova: $H_{df=2}$=20,27, p<0,0001). However, median values for subfamilies are still quite tightly clustered around midnight (Smerinthinae 6h, Sphinginae 7,5h past sunset). Median arrival times also differ between sites (KW-Anova: $H_{df=11}$=130,8, p<0,0001), which is most

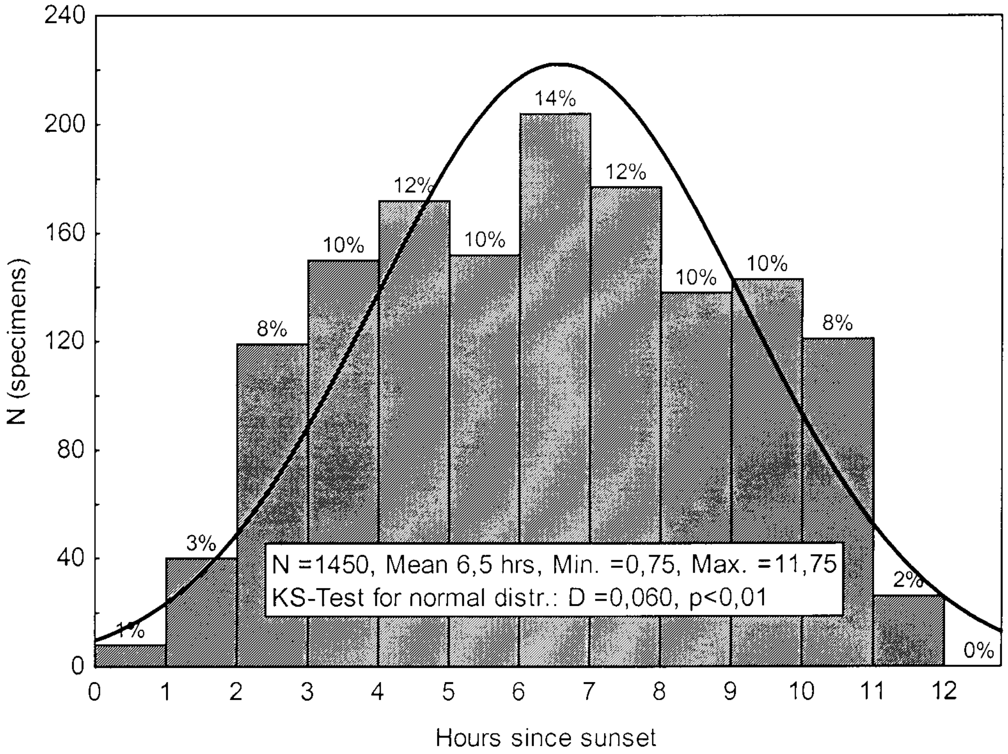


Figure 2.7 shows the distribution of arrival times of Sphingidae specimens in Borneo and in Peninsular Malaysia as a function of sampling time. Despite a symmetric distribution around midnight data do not fit a normal distribution.

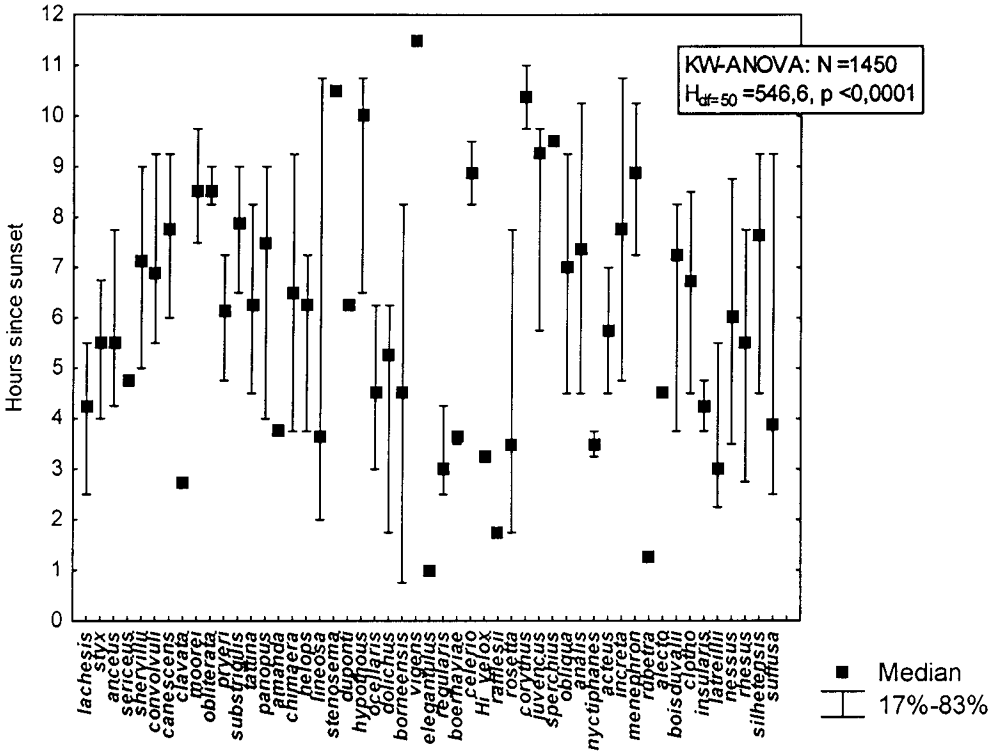


Figure 2.8 shows median arrival times of 50 Sphingid species in Borneo and Peninsular Malaysia. Different species have clearly and significantly differing flight times during the night.

probably the effect of different moonlight and weather conditions. Over the range of sample sites, however, these differences are levelled out as figure 2.6 shows a very symmetric distribution.

If flight times are adaptive, several hypothetical factors can be suspected to influence flight time differentiation:

a) Adult food choice: Species with similar adult food habits might separate in flight time to avoid competition (e.g. for flower nectar). Smerinthinae might then be expected to show more overlap in flight time, as most species of this subfamily do not feed as adults (e.g. Lemaire & Minet 1998, Kitching & Cadiou 2000).

b) Avoidance of mating in closely related taxa might be a reason for differences in activity patterns. Species within genera should have less flight time overlap than average species couples.

c) Nightly predation (by bats) in Sphingids is mainly avoided by fast flight. With decreasing temperatures during the night, larger species can maintain their flight muscle temperature, hence their agility, more easily than small-bodied species. Thus, smaller species should fly earlier in the night than large species.

Pianka's niche overlap of flight times was calculated for all Sphingidae [50 spec.], 3 subfamilies, and intra-genera comparisons within the genera *Ambulyx* [5 spec.], *Theretra* [4 spec.] and *Acosmeryx* [2 spec.] (see Southwood & Henderson 2000, computed with

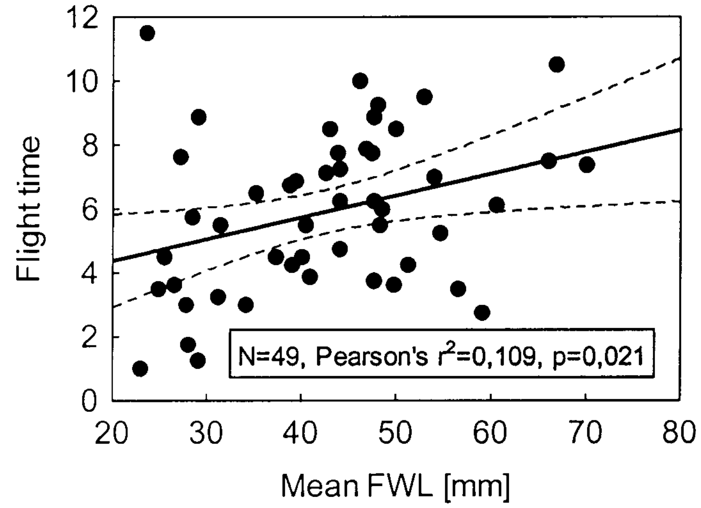


Figure 2.9 shows a linear regression (±95% CI) between body size (measured as mean forewing length) and median flight time (see figure 8). However, the relationship is spurious due to phylogenetic non-independence of the body size data (see text).

Programs for Ecological Methodology, Kenney & Krebs 2000). Mean values range around 0,6 for all Sphingidae and the subfamilies Smerinthinae and Macroglossinae, <0,5 for the subfamily Sphinginae, and >0,7 for the intra-genera comparisons. No indications for a higher overlap in Smerinthinae (hypothesis a), nor a lower overlap for within-genera comparisons (hypothesis b) was found (no differences between groups, Anova: $F_{df=4}$=1,174, p=0,323; statistical comparisons are problematic due to an artificial inflation of sample sizes from pair-wise calculations, but the non-significance of comparisons remains valid). There is a tendency (figure 2.9) for smaller species to fly earlier than large species (body size was measured as mean forewing lengths, which is a good surrogate for body mass within a group of similar body architecture; Loder et al. 1998, Schoener 1980). However, correlations of species' characters might not be statistically independent because of their common phylogenetic history (see e.g. Garland et al. 1999 for a review). The phylogenetic signal in data was tested with a randomization test (1000 runs), using the program *Phylogenetic Independence 2.0* (Reefe & Abouheif 2003, see also Abouheif 1999, Freckleton et al. 2002). Hawkmoth phylogeny was based on an updated version of the systematic in Cadiou & Kitching 2000 (I.J. Kitching pers. com.), allowing for unresolved nodes where applicable. While in body size data a clear phylogenetic signal was detected (p=0,001 for phylogenetic independence), no signal was detected in flight time data (p=0,430). Independent contrasts (Felsenstein 1985) were calculated using the computer program *Phylip 3.61* (Felsenstein 2004; all branch length set to 1 except unresolved nodes, which were set to 0,0001). A correlation of independent contrasts for body size and flight time is not significant (N=48, R^2=0,017, p=0,376), nor is a correlation of contrasts for body size with uncorrected data for flight time (N=48, R^2=0,002, p=0,769), using contrasts for a neutral, star-like phylogeny (see also Rheindt et al. 2004 for methods). These analyses indicate that the relation between flight time and body size (figure 2.9) is spurious.

4) 'Seasonality' and temporal change

Comparisons of the 'within-habitat' diversity of re-sampling sessions (figure 2.10) showed a remarkable constancy of measures; only at one site (CRO1) a significant change in diversity could be observed, even though the species inventory in both samples was identical (table 2.6). No influence of 'seasons' (see table 2.5) on diversity differences could be observed, indicating that changes in the structure of hawkmoth assemblages are either random or

Site	Sample I	Sample II	Sample III	Sample IV
DV1	Jun 2001 (2)	Dec 2001 (3)	Mar 2003 (1)	Dec 2003 (3)
CRO1	May 2001 (2)	Nov 2001 (3)		
POR1	Jan 2002 (3)	Feb 2003 (1)		
POR8	Jul 2001 (1)	Jan 2002 (3)	Feb 2003 (1)	

Table 2.5 shows re-sampling sessions (4-9 nights each) at four sites in Sabah, Borneo. Numbers in brackets indicate 'seasons' based on rainfall measurements at Danum Valley Field Centre (see Marsh & Greer 1992), but the assessment of seasons is based on means of 17 instead of 6 years of meteorological data collection (data not shown, G. Reynolds pers. com.): (1) = 'Dry Seasons' February-April, July-September (<230 mm rainfall per month), (2) = 'South-West Monsoon' May-June, (3) = 'North-East Monsoon' October-January (>250 mm). Climate patterns might be different in other parts of Borneo (e.g. Walsh & Newbery 1999, Kato et al. 1995, Kitayama et al. 1999).

directional in a longer time scale than one year (see chapter 3.1). Measures of between-session similarity of the sampled assemblages are relatively high, particularly for NESS-indices (Grassle & Smith 1976) which are not biased (towards lower values) by incomplete species inventories as Sørensen-indices are (Southwood & Henderson 2000). If common species are weighted high for calculation of NESS *(m=1)*, it seems that primary forest sites (DV1, POR1) are more stable than disturbed sites. This pattern, however, breaks down if rare species are weighted higher at *m=30*. All NESS *(m=30)*-values are >0,85 for within-site comparisons of sessions (see also Novotny et al. 2002).

Relative abundances of sampled species were correlated to each other (table 2.7) to assess how well sampling in one session reflects the rank order of species in other sessions at a site. All relevant correlations are highly significant, though R^2-values are not particularly high. Within-site correlations have clearly higher R^2-values than between-site correlations (Mean±SD, within site: R^2=0,712±0,08; between sites: R^2=0,473±0,10; statistical tests were not applied as this presentation spuriously inflates sample sizes). Thus, although there are considerable changes in relative abundance for single species, assessments of rank order of the species in an assemblage remain quite constant.

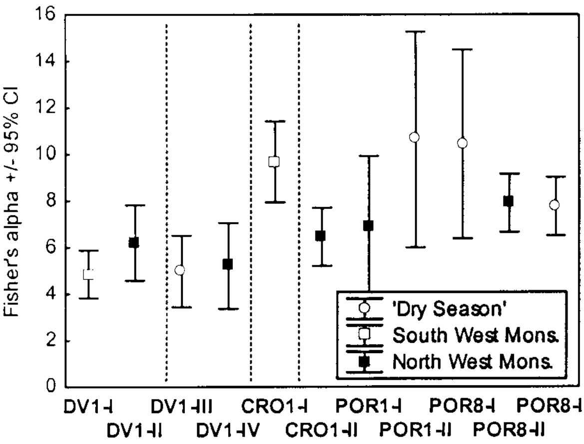


Figure 2.10 shows values for Fisher's α (±95% confidence interval) as a measure of within-habitat diversity for re-samples of four sites in north-eastern Borneo (see table 1). Only at one site (CRO1) a significant difference in diversity between re-samples with a site (dashed lines) can be observed. There is no indication for systematic influences of season (see table 5) on diversity. Fisher's α (±95%CI) for pooled sample sessions are: DV1: 5,98±0,99, CRO1: 8,15±1,23, POR1: 8,65±2,46, POR8: 7,97±1,05. All samples fit the *logseries*-distribution sufficiently good to justify the use of Fisher's α (Southwood & Henderson 2000).

Site	Re-samples	Sørensen (Mean±SD)	NESS (*m=1*) (Mean±SD)	NESS (*m=30*) (Mean±SD)
DV1	4	0,83 ± 0,18	0,95 ± 0,04	0,88 ± 0,04
CRO1	2	1,00	0,80	0,86
POR1	2	0,67	0,86	0,92
POR8	3	0,87 ± 0,12	0,78 ± 0,07	0,94 ± 0,02
HOA	10	0,47 ± 0,24		

Table 2.6 shows measures of between-habitat similarity between sampling sessions of four sites in Borneo. All indices range from 0 (no species in common between sessions) to 1 (identical samples). While Sørensen-indices consider only presence-absence data (Southwood & Henderson 2000), NESS-indices (Grassle & Smith 1976) use quantitative data with increasing weight on rare species with increasing *m* (see e.g. Brehm & Fiedler 2003 for an assessment of between-habitat diversity measures). For comparison, between-habitat diversity of 10 samples (within 12 months) in seasonal northern Vietnam (Hoang Lien Nature Reserve, data from T. Larsen, pers.com.) is presented.

	DV1-I	DV1-II	DV1-III	DV1-IV	CRO1-I	CRO1-II	POR1-I	POR1-II	POR8-I	POR8-II
DV1-II	**0,812**									
DV1-III	**0,673**	**0,624**								
DV1-IV	**0,650**	**0,701**	**0,576**							
CRO1-I	**0,555**	**0,572**	0,465	0,515						
CRO1-II	**0,493**	**0,586**	0,379	0,410	**0,740**					
POR1-I	**0,603**	**0,650**	**0,577**	**0,525**	**0,657**	**0,621**				
POR1-II	**0,598**	**0,643**	**0,504**	0,425	**0,525**	**0,549**	**0,676**			
POR8-I	0,359	0,430	0,272	0,274	0,419	0,388	0,309	0,393		
POR8-II	0,425	**0,510**	0,395	0,409	0,422	0,458	**0,538**	0,474	**0,767**	
POR8-III	0,373	0,441	0,370	0,400	0,478	0,449	0,453	**0,534**	**0,775**	**0,842**

Table 2.7 shows R-values for Spearman rank correlations of relative abundances of species across 11 (re-)sampling sessions in Borneo. All correlations are significant (N=58, p<0,05), values in bold print mark correlations at p<0,0001. The latter include all within-site correlations of sessions (in boxes).

Discussion

Attraction radius of light sources

In the experimental part of this study it was shown for 18 species of Sphingidae, as well as some species of the Geometridae and Noctuidae, that the effective attraction radius of a 125 Watt MV-lamp is indeed relatively low with distances below 30 metres. This confirms what most previous studies found with different methods, species and habitats (e.g. Muirhead-Thompson 1991, Bowden & Morris 1975, Onsager 1973, Plaut 1971, Meineke 1984, Kovács 1958). Even for hawkmoths, which probably form the upper limit of lepidopteran flight strength and speed, there is no indication that light trapping draws moths from distances so great that investigations on local habitats were 'polluted' by specimens from far away. Occasionally specimens were found at light sources far off their typical habitat (e.g. on ships far off the next coast; I.J. Kitching, pers.com.), but there is no indication whatsoever that such specimens were artificially drawn out of their natural habitat by the light.

Differences between taxa

A comparison between families with considerably different body sizes and shapes revealed significant differences in return behaviour and attraction radius. Fiedler et al. (unpublished data, pers. com.) found in similar mark-release experiments in Germany that body size has a significant effect on return rates of Geometroidea (though not in other taxa). Therefore, results of light trapping studies from taxonomically and/or morphologically very divers samples must be viewed very careful, as relative abundances at the light might not reflect relative abundances under natural flight conditions. Within the relatively uniform taxon Sphingidae, on the other hand, comparisons of 18 species did not show any non-random differences in return behaviour despite a considerable sample size of over 1.300 released specimens (see table 2.2). While it is known that some differences between species must exist (e.g. some species do not come to light at all; Butler et al. 1999 found substantial differences between blacklight and malaise traps for three North American hawkmoth species), these differences might often be diluted beyond significance by a high variability in attraction radii (see below) during natural trapping conditions. It might be argued that in this study the concentration on relatively common species (for the obvious reason of attaining sufficient sample sizes) might have neglected systematic differences between common and rare species. Generally, a missing effect can never be proven beyond doubt, but there is no indication to assume that there is a systematic (e.g. taxonomic) difference in attraction radius between rare and common species.

The species-abundance distribution in a large number of light-trapping samples of hawkmoths from Southeast-Asia fit the lognormal distribution very well (chapter 3.2). This or similar mathematical distributions have been found in samples of a large number of organisms (e.g. Robinson 1998), including sampling procedures which are beyond any doubt free of sampling errors (e.g. counting tree seedlings in sample squares, Hubbell 2001). If the lognormal and related distributions have any biological significance (e.g. Hubbell 2001, Hengeveld & Stam 1978) and are not merely a statistical artefact inherent to any heterogeneous data set, then massive biases of light trapping would have distorted this relationship for night-active Lepidoptera sampled in this way.

High variability in data: a methodological artefact?

The release experiments revealed a large variation in return behaviour, which was also evident from observations during field work: while some specimens could be observed to fly in a straight line towards the light after release at distances of up to 130 metres, other specimens did not return at all. The failure to find species-specific differences in light attraction might be attributed to this variability rather than homogenous measures of attraction (see e.g. figure 2.3). Therefore it is a crucial question for the interpretation of results to what degree such variation might be caused by handling effects or other problems of the experimental design. Obvious handling effects could repeatedly be observed in *Daphnusa ocellaris*, which walked away after release rather than to fly, and was consequently excluded from all analyses. However, it was not completely surprising to find odd behaviour in this species, as it is an 'unusual' hawkmoth in a number of other behavioural traits: In Borneo, it is the only species that is frequently encountered in the undergrowth of the forest, whereas all other species tend to fly in the open airspace above the tree canopy (Schulze & Fiedler 1997). Furthermore, its relatively small thorax makes it considerably weaker in beating its wing than species of comparable size (pers. obs. during handling). The observed behaviour can probably be interpreted as a predator escape tactic after an unsuccessful first attack of a bat. In no other hawkmoth species such behaviour was observed.

Predation by bats around the light was high, and occasionally it could be observed that released moths were caught by bats just before returning to the light. While this reflects the situation at most trapping sites in Southeast-Asia, it might mean that 'physiological' attraction radii are slightly larger than 'ecological', bat-influenced measures of the radii. Weather, moonlight and temperature varied within as well as between sampling nights and might be responsible for a large part of variation in measured attraction radii. All three parameters are known to influence total catch size (e.g. Yela & Holyoak 1997) and might be suspected to influence the flight activity of moths as well as the attraction radii of light sources. Fiedler et al. (pers. com.) found effects of temperature on attraction radii of Geometroidea, albeit in temperate Germany, where temperatures vary much more than in tropical lowland areas. However, just like bat predation, such variability only reflects realistic sampling conditions and is therefore not a methodological problem. Whatever physiological differences there might be to influence differences in response to light between species, natural variation in conditions during realistic sampling procedures seems to reduce them to a non-directional 'noise' that will most probably not produce any artefact results in ecological studies.

Completeness of samples

Using the *Chao1*-estimator (Colwell 2000) as a measure of true species richness in a habitat, it was found that short term (<10 nights), high intensity light trapping (125W MV-lamp, all night hand-sampling) can yield a surprisingly complete picture of the species assemblage that is present in a habitat at a particular time (excluding the day-active taxa, of course). An average of ¾ of the expected species (and often much more) could be inventoried with this method. Sphingidae are not a very specious taxon in Southeast-Asia (e.g. species numbers from Borneo: 113 Sphingidae (Beck & Kitching 2004), compared to ca. 1000 described Geometridae (Holloway 1993a, 1996a, 1997a), but a relatively high degree of available 'background information' even among tropical species (taxonomy, distribution, host plants, etc; e.g. Kitching & Cadiou 2000) makes them a very attractive group for ecological research among the Lepidoptera.

It is difficult to judge how reliable *Chao1*-estimates really are. Estimates increased with increasing S_{obs} within some sites (see Schulze & Fiedler 2003a for a similar effect on Fisher's α of Pyralidae), even though they often reached relatively stable values with addition of the last 1-2 sample nights (see figure 2.5). Alternative estimators (see results) came to very similar figures of expected species, and figure 2.6 indicates that estimates are generally in a realistic range. Thus, results might be tentatively considered credible, although only more studies on Colwell's (2000) estimators can really judge their value as predictors of true species richness.

Moreno & Halffter (2000) used randomised species accumulation curves to determine asymptotes of species inventories for neotropical bat assemblages, which were suggested to be used for the comparison of incomplete samples, across different sampling methods or sampling efforts. This was criticised by Willot (2001; but see Moreno & Halffter 2001), who pointed out that (1) the number of sampled individuals is a better measurement of sampling effort than the number of sampling units, and (2) that the method is not suitable for high diversity taxa where only a small fraction of a local assemblage has been sampled. The *MMMeans* method of richness estimation (Colwell 2000, Chazdon et al. 1998) follows a similar approach by fitting an asymptotic Michaelis-Menten type curve to randomised species accumulation curves. *MMMeans*-estimates were generally very similar to *Chao1*-estimates in this study. Figure 2.5 shows an example of species accumulation curves. Estimates of total species richness from *Chao1* generally were in an acceptable range when viewing randomised species accumulation curves, which adds credibility to both approaches.

Flight times

The analysis of flight times shows that it is crucial to stay out all night in order to sample Southeast-Asian hawkmoth communities successfully and completely. Not only does the greatest number of specimens come around midnight to the light (and keep coming until dawn), but a shorter sampling period would also systematically under-represent certain species as median flight times vary significantly between species. The ability of Sphingidae to warm up their flight muscles by shivering gives them the opportunity to make their flight activity relatively independent of ambient temperatures, at least under the moderate temperature changes of a tropical night.

It remains to be seen from similar data on other taxa, if 'niches' in flight time are a general feature of moth assemblages. Anecdotal information points into this direction – Saturniidae, for example, are said to be found in numbers only after midnight (C.H. Schulze, pers. com). No reasons for these flight time niches could be confirmed from Sphingid data, though the body size of early-flying taxa tends to be smaller than that of late-flying taxa. Studies on other organisms suggest that partitioning of activity times is only rarely caused by competition or predation, and that endogenous rhythmicity may be an evolutionary constraint (e.g. Kronfeld-Schor & Dayan 2003). No decline in the number of Sphingidae specimens was found under conditions of heavy rain (nor for other groups, though this was not quantified). No moths might be flying during the peak minutes of a tropical rainstorm, but they still keep coming under very unpleasant sampling conditions. Thus, breaks from a sampling schedule due to heavy rain (which are commonly reported in the literature) cannot be excused by low sampling success, although more fragile taxa might by damaged beyond determination by wet equipment.

Seasonality and temporal change

No evidence of 'seasonality' was found in Sphingid assemblages from north-eastern Borneo, though it has to be considered that data were too limited for an application of rigorous tests of circular patterns (e.g. Wolda 1988). Previous studies suggested that not only in tropical habitats with clear wet and dry seasons (e.g. Frith & Frith 1985, Janzen 1993), but also in less seasonal regions (Novotny & Basset 1998, Intachat et al. 2001, Wolda 1978) insect abundances can fluctuate considerably as an effect of changes in precipitation. Data suggests that while there are considerable changes of relative and absolute abundances of species between sampling sessions, measures of diversity (figure 2.10), community structure (table 2.6) and the rank order of species (table 2.7) are not dramatically different. A number of other authors also concluded that temporal changes did not disturb measures of community structure for ants in Borneo (Brühl 2001) or Lepidoptera in Sulawesi (Barlow & Woiwod 1993) and New Guinea (Novotny et al. 2002). Thus, in the absence of clear seasonal patterns (see also Walsh & Newbery 1999), it was concluded that short-term samples probably give reasonably good data for analyses of local assemblages of Sphingidae in Borneo – even though it has to be kept in mind that assemblages might change over timescales of several years (analysis of data from Borneo, chapter 3.1). For a few species (*Theretra rhesus, T. latreillii, T. insularis, Daphnis hypothous, Marumba juvencus, Enpinanga borneenis, Cechenena lineosa*) there are indications of larger population fluctuations from the data and from comparisons with older literature (e.g. Holloway 1976, 1987a, Tennent 1991).

Conclusions

From the experimental and empirical data that were presented above, the following conclusions and methodological advises can be drawn:

1) For complete and efficient sampling of Sphingidae (at least in Southeast-Asia), hand-sampling at a light source during the whole night is necessary. Shorter nightly sampling sessions miss a considerable number of specimens, and – more importantly – might specifically miss species with particular flight times, which would bias data.

2) Under these conditions, a week of sampling will usually yield over 100 specimens, which often represent more than ¾ of the expected species in a habitat (excluding day-active species). Pre-condition to this is an adequate choice of sampling site, which should sample from some open airspace rather than dense vegetation (Schulze & Fielder 1997). Seasonality of assemblages can probably be neglected for practical purposes, though care has to be taken when including data from older sources or from more seasonal regions of Southeast-Asia.

3) There is no indication that specimens are not sampled locally, but drawn from some distant natural habitats to the sampling site by the light. A 125 Watt mercury-vapour bulb has a 50 percent attraction radius of less than 30 metres (which confirms older measures from the literature, see above), so even highly active, fast-flying taxa such as Sphingidae can be very locally sampled. However, individual specimens might fly far from their normal (breeding) habitat for natural reasons (e.g., dispersal, migration).

4) No evidence was found that species within the family Sphingidae differ significantly in their attraction to light (excluding day-active species that do not come to light at all). While this does not generally rule out the possibility of such effects, natural variation under normal sampling conditions might effectively level out such differences. It is tentatively concluded that abundances at light sources largely do reflect relative abundances (or rather flight activity) in a habitat. However, wherever there is an option of comparing relative abundances at light with other measures of relative species abundance (e.g., counts of caterpillars from random samples), then these should be employed and critically discussed.

5) There is strong indication that attraction towards the light differs between higher taxonomic units such as Lepidopteran families. Large differences in body size or shape might be a key predictor for the dimension of such differences. Data for taxonomically or morphologically divers assemblages should be critically explored for potential biases resulting from different attraction radii of light. In biodiversity studies that compare different habitats, for example, it should be explored if different taxonomic sub-units follow similar patterns before they are presented as common trend from a pooled data set.

CHAPTER 3 – LOCAL ASSEMBLAGES

CHAPTER 3.1 - LOCAL SPECIES DIVERSITY

Abstract

Sphingid biodiversity was compared in a large number of light-trapping samples on Borneo and elsewhere in the Indo-Australian region, using own quantitative light-trapping samples supplemented by published and unpublished data.

No effects of anthropogenic habitat disturbance on the within-habitat diversity (measured as Fisher's α) were observed, but the faunal composition of assemblages differs significantly under varying degrees of disturbance. Altitude, the year of sampling and the sampling regime (full night vs. part of the night) were identified as further parameters that influence the composition of local samples.

The frequency of subfamilies in samples varies under different disturbance regimes: Smerinthinae decline along a gradient from primary habitats to heavily disturbed sites, whereas Macroglossinae show the reversed trend.

Connections between the reactions of subfamilies to disturbance and altitude, and life-history differences between the subfamilies are discussed: Capital breeding Smerinthinae might be commoner and more specious in stable primary habitats, while income breeding Macroglossinae are probably adapted to thrive in ephemeral, disturbed habitats.

Turnover rates in different habitat types give no indication that disturbed sites have a lower β-diversity than primary forests, i.e. they are not more homogenous with reference to their Sphingid fauna.

Introduction

Biodiversity research is to a large extent concerned with the documentation and understanding of the influence of habitat disturbance on the species diversity and composition of biological communities (e.g. Lawton et al. 1998, Lovejoy 1994). To understand how biological communities react to human habitat destruction or fragmentation is not only academically interesting, but of vital interest for ecosystem management, which undoubtedly will be of increasing concern for human societies in the future (see e.g. Linsenmair 1997, Ingram & Buongiorno 1996, Dotzauer 1998, Mawdsley 1996, Hector et al. 2001), considering especially the immense damage that is done to today's tropical ecosystems (Bowles et al. 1998, Sodhi et al. 2004). However, time- and manpower-constrained research usually involves investigation of one or a number of 'handpicked' taxonomic groups, of which is inferred that they reflect reactions of other groups of organisms (Hammond 1994). This assumption has only rarely been tested within the same sampling sites (Lawton et al. 1998, Beccaloni & Gaston 1995, Schulze et al. in press), and while local diversity for a majority of taxa is diminishing with increasing disturbance, reactions of different groups are often quite dissimilar in detail (e.g. termites: Gathorne-Hardy et al. 2002a, Eggleton et al. 1997, scarabid beetles: Holloway et al. 1992, chrysomilid beetles: Wagner 1999, leaf litter ants: Brühl 2001, canopy invertebrates: Simon & Linsenmair 2001, Floren et al. 2001, vertebrates: Johns 1992, Lambert 1992, mantids: Helmkampf et al. in press, butterflies: Ghazoul 2002, Hamer et al. 1997, see also Lawton et al. 1998, Schulze et al. in press). Each taxon has certain specific habitat requirements (see also Dennis 2003, Summerville & Crist 2003) that often lead to species loss with the disturbance of tropical rainforest habitat, but may sometimes and for some taxa also lead to inverted patterns or reactions that cannot be explained with disturbance alone (e.g. Beck et al. 2002, Helmkampf et al. in press.) For example, within-habitat diversity of Geometrid moths in north-eastern Borneo seems to be largely ruled by undergrowth plant diversity (Beck et al. 2002), which leads to a general decline with increasing forest disturbance, but also leads to primary-forest-like species diversity in some moderately disturbed habitats that have a high undergrowth plant diversity (see also Chey et al. 1997, Intachat et al. 1997, 1999).

Lepidopteran diversity and its change under different disturbance regimes or habitat gradients has been intensively investigated in northern Borneo (Holloway 1976, 1984, Holloway et al. 1992, Chey et al. 1997, Schulze 2000, Beck et al. 2002, Beck & Schulze 2000, Willott 1999, Willott et al. 2000, Hamer & Hill 2000, Schulze & Fiedler 2003a, Fiedler & Schulze 2004) and elsewhere in the Indo-Australian tropics (Intachat et al. 1999, Holloway 1987b, 1998a, Hill et al. 1995, Fermon et al. 2005). While for some groups (e.g. Geometridae, Pyralidae, Arctiinae, fruit-feeding butterflies) clear negative effects of habitat disturbance on species diversity and community composition were found (particularly when changing from forests to heavily disturbed or open agricultural land, e.g. Schulze 2000, Beck et al. 2002, Willott 1999), night-active hawkmoths were found to be apparently inert to habitat disturbance, both with regard to within-habitat disturbance as well as community composition (Schulze & Fiedler 2003b).

Hawkmoths are ecologically important (e.g. as pollinators: Haber & Frankie 1989) and are a suitable 'model group' for ecological investigations (e.g. Sutton & Collins 1991, Pearson

1994) due to the availability of a comparatively large amount of background information (taxonomy, host plants, distribution; e.g. Kitching & Cadiou 2000, Pittaway & Kitching 2003, Beck & Kitching 2004) that is matched for tropical invertebrates only by butterflies (e.g. Fiedler 1998). Reactions of their within-habitat diversity and community composition to anthropogenic disturbance and other habitat gradients (e.g. altitude) are a crucial point for the understanding of ecological processes on a community level. These reactions were re-evaluated for hawkmoths in Borneo and elsewhere in Southeast-Asia, using a larger dataset and somewhat different methods than Schulze & Fiedler (2003b; see also methods and discussion). Particular questions to the data set were:

1) Are the within-habitat diversity and faunal composition of Sphingid assemblages in Borneo (and elsewhere in Southeast-Asia) really not influenced by habitat disturbance?

2) How do other environmental gradients, such as altitude or geographic position, influence local hawkmoth assemblages?

3) Are there differences between taxonomic sub-groups of the Sphingidae in their reactions to environmental gradients? Such effects were found in an analysis of an altitudinal gradient on Mt. Kinabalu (North-eastern Borneo; Schulze 2000, see also Schulze et al. 2000) and might also play a role in the biogeographical patterns of hawkmoths throughout the Malesian archipelago (chapter 4.1).

Methods

Field methods and data sources

During an extensive light trapping program Sphingidae were quantitatively recorded in 178 sample nights on various sites across Southeast-Asia (see table 3.1, appendix I). The moths were attracted to a generator-driven 125 Watt mercury-vapour lamp that was placed inside a

Region	No. sites	No. specimens	No. own sample sites	Sources (published)	Sources (pers. com.)
Borneo	57	12.333	23	Chey 1994 Chey 2002a Holloway 1976 Schulze 2000 Tennent 1991 Zaidi & Chong 1995	G. Martin (NHM London) J.D. Holloway*) (NHM London)
Peninsula Malaysia	3	284	1		Azmi M. (FRIM Kepong)
Northern Vietnam	1	3.223			T. Larsen
Flores	3	324	3		
Lombok	1	29			U. Buchsbaum (ZSM München)
Luzon	2	45			W. Mey (NKM Berlin)
Negros	1	36			W. Mey (NKM Berlin)
New Guinea	6	480			H.v. Mastrigt U. Buchsbaum (ZSM München)
Seram	11	650			J.D. Holloway **) (NHM London)
Sulawesi	5	147			J.D. Holloway***) (NHM London)
Taiwan	3	125			W. Mey (NKM Berlin) U. Buchsbaum (ZSM München)

Table 3.1 shows sources of quantitative light-trapping data for Sphingidae in Southeast-Asia.
*) see Holloway 1984 **) see Holloway 1993 ***) see Holloway et al. 1990

white gaze cylinder of ca. 1,7 metres height. Moths were caught by hand at the light or in the nearby vegetation, identified (Holloway 1987a, D'Abrera 1986, Kitching & Cadiou 2000), individually marked with waterproof pen and stored inside the gaze cylinder until dawn, when they were released. Individual marking ensured that pseudoreplicates, which could be caused by re-catches in following nights (see e.g. Beck & Schulze 2000), were avoided. Only if species identification was unsure (<10 % of specimens) the moths were killed and stored for further determination, or digital photos were taken for identification aided by a specialist. Sampling was carried out all night and at all weather conditions. Each site was sampled for 3-9 nights in a row, which probably yields an average of more than ¾ of the total species richness at each site (chapter 2). Four sites in Borneo were re-sampled up to 4 times to assess effects of seasonality (chapter 2), but data of sampling sessions at the same site were pooled for analyses of species diversity. Three combined 15 Watt blacklight tubes (*Sylvania blacklight-blue*, powered by 12 Volt 'dry-fit' batteries) were used on the few sites where logistic conditions forbade the use of a generator. Most sites were chosen to allow sampling from open airspace, in open landscapes or in the forest canopy (accessed either by platforms or steep slopes or cliffs), as Sphingidae are known to avoid flying in dense undergrowth (Schulze & Fiedler 1997). Sampling sites were situated as deep as logistically possible (at least ½ km) inside a habitat type in order to minimize the overlap of faunas from neighbouring habitats.

Additionally to own samples published as well as unpublished data (table 3.1) were compiled which led to quantitative light-trapping data for 93 sites from Southeast-Asia (see appendix I, table 3.1: 17.676 specimens, 159 night-active species) and includes most of the data used in Schulze & Fiedler (2003b). For Borneo alone, 57 sites (12.333 specimens, 77 species) have been analysed. Generally, only sites with a minimum of 20 individuals were considered for analyses. Sampling was mostly carried out in similar short-term, high intensity light trapping sessions as described above, but light sources, sampling schedule and duration differed between sources. All data were corrected for a unified taxonomy, following an updated version of Kitching & Cadiou (2000; I.J. Kitching, pers. com.). Data for mainly day-active genera (such as *Macroglossum, Cephonodes* & *Sataspes*) were generally excluded if they were occasionally caught at light.

From own observations or site descriptions of other authors, habitats were grouped in three disturbance classes: (1) *Primary habitats* without any significant human disturbance were usually primary rainforests. (2) *Secondary habitats* ranged from selectively logged forests through secondary forests to sites which were at least partly forested. (3) *Heavily disturbed* sites consisted of anthropogenically opened landscapes, often near villages, agricultural sites or plantations. Not for all sampling sites complete habitat descriptions could be obtained. Smaller sample sizes compared to the total number of sites in some tests are due to missing values for altitude or disturbance class for some samples. All sampling sites are listed in appendix I.

Biodiversity statistics

Species richness or diversity in a habitat cannot be measured directly as the number of observed species if samples are incomplete, which is the normal condition in entomology, particularly if tropical taxa are concerned (Gotelli & Colwell 2001, Lande 1996). Furthermore, absolute abundance of specimens at light is influenced by variables that are not related to the habitat (e.g. weather, moonlight; Yela & Holyoak 1997) and can therefore not be used directly for analysis. An appropriate measure has to be employed which is independent of the sampling effort or –success and gives a reliable, comparable estimate of diversity. For this purpose, Fisher's α (see e.g. Wolda 1981) was calculated for every site. This well established index of diversity has proven robust and suitable for comparisons of biodiversity in a number of comparative studies and is considered the best index of within-habitat diversity (Wolda 1981, Taylor 1978, May 1978, Kempton & Taylor 1974, Hayek & Buzas 1997, Southwood & Henderson 2000). The underlying assumption in the calculation of this index, a resemblance of the species-abundance relation to the *logseries*-distribution, was met in 89 of 93 sites (see chapter 3.2; KS-test, $p>0,05$), though Fisher's α has also proven relatively robust if this assumption is violated (Hayek & Buzas 1997). To assess the reliability of α-values, 95 percent confidence intervals were computed based in the estimate of α's variance by Anscombe (1950). Fisher's α and its confidence intervals were computed with *Programs for Ecological Methodology* (Kenney & Krebs 1998).

NESS($m_{\max}=10$)-indices of faunal similarity (Grassle & Smith 1976) were used to investigate changes of the local species assemblages due to disturbance or other factors. This measure considers quantitative data (rather than just presence/absence of species) and is not biased by incomplete samples (Grassle & Smith 1976), which is a common problem with other between-habitat diversity measures such as Jaccard's or Sørensen's index (Wolda 1981). By choice of its parameter m, rare species can be weighted lower (low m) or higher (high m). NESS-indices were used to produce non-metric Multidimensional Scaling plots (MDS, see Minchin 1987 for advantages over other ordination techniques), which allow to display and test distance data with a reduced number of dimensions (Cox & Cox 1994, Legendre & Legendre 1998, Pfeifer et al. 1998). In a recent comparison Brehm & Fiedler (2004) suggested that non-metric MDS plots based upon NESS with the highest possible m are superior to other ordination methods in order to display quantitative ecological data. Dimension values can be tested for the influence of habitat parameters by standard statistical methods (Cox & Cox 1994). NESS-values were calculated with a computer program provided by S. Messner (pers. com.), non-metric Multidimensional Scaling and all standard statistics were computed with the program *Statistica 6.1* (StatSoft 2003).

Multiple statistical tests from the same data set can lead to spurious results and were controlled by the method of Hochberg (1988). All major results fulfil these conditions, but re-tests of the same topic (e.g. tests on data subsets with more homogenous data) were not considered for control (see also Moran 2003).

Results

Within-habitat diversity

A comparison of disturbance classes did not reveal any pattern that would indicate an influence of anthropogenic disturbance on the within-habitat diversity of Sphingidae in 57 samples from Borneo (see figure 3.1). A comparison of median values of Fisher's α between the three classes confirms this conclusion (Kruskal-Wallis Anova: $H_{df=2}$=0,395, p=0,825). Similarly, no clear and significant effects of altitude (with data ranging from sea level to 2600 metres a.s.l.) could be found (figure 3.2), but a fitted curve (negative exponential least squares method) suggests a mid-elevational peak of Fisher's α above 1000 metres altitude. A restriction of the analysis to data from the 30 sampling sites with more than 80 individuals, or to the 17 sampling sites with more than 150 individuals, did not reveal any clearer patterns, so small samples can be ruled out as a reason for artefacts.

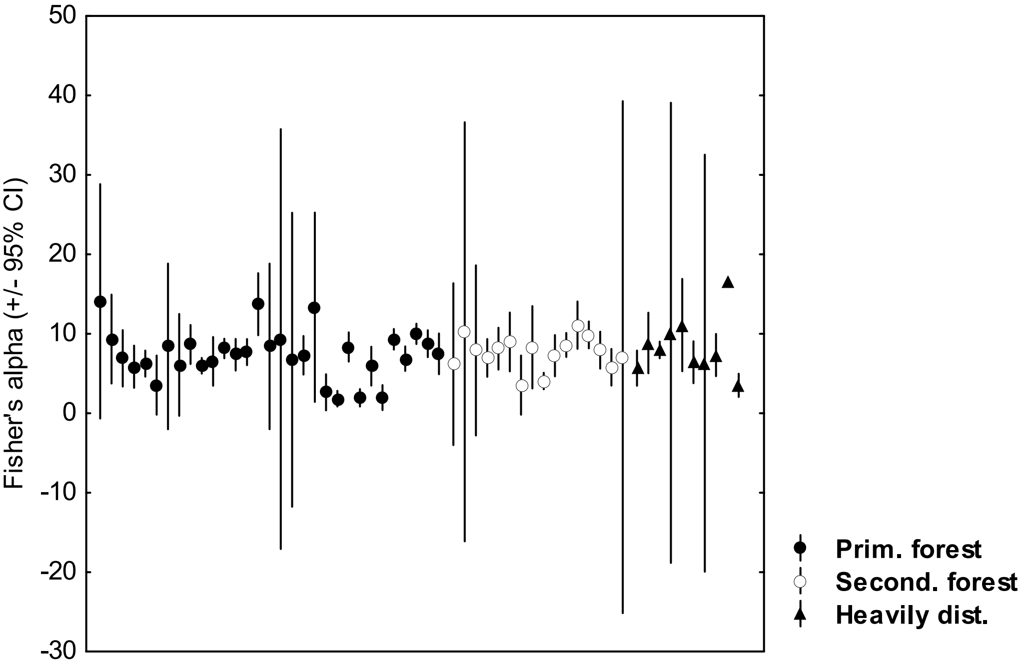


Figure 3.1 shows Fisher's α (±95% confidence intervals) for 57 sites on Borneo. No significant differences between sites can be observed (see text). Sample sizes and further details of all sites can be found in appendix I.

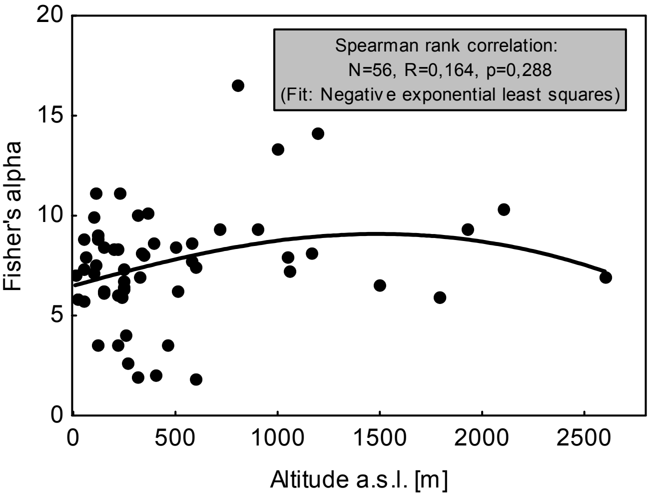


Figure 3.2 plots Fisher's α of 56 sampling sites on Borneo as a function of altitude. No significant effects can be observed, although the fitted curve suggests an increase of diversity in medium elevations (see discussion).

Data from other islands cannot be directly compared to the Borneo samples as there are significant differences in median Fisher's α between regions (KW-Anova: N=93, $H_{df=10}$=27,091, p=0,003). There are no effects of latitude in the data, but diversity is decreasing with increasing longitude (Spearman rank correlation: N=93, R=-0,282, p=0,006), which is probably an effect of distance to continental Asia and of the biogeography of Malesia (chapter 4, Beck & Kitching 2004). However, diversity measures within other regions (figure 3.3) do not give any indication that the inertness of Sphingid diversity to habitat disturbance is specific to Borneo.

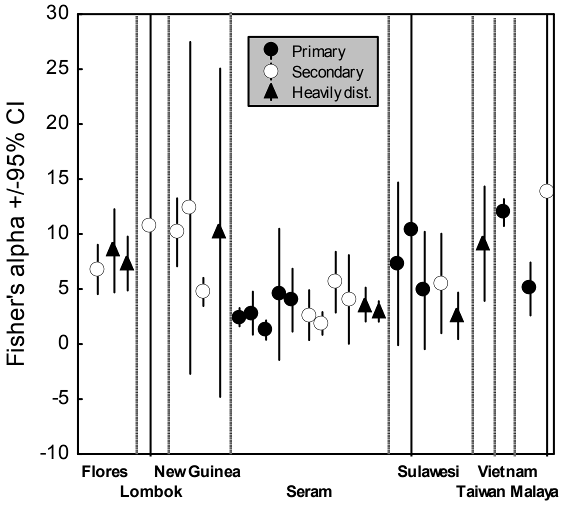


Figure 3.3 shows Fisher's α (±95% confidence intervals) for local samples for several regions (separated by dashed lines) in Southeast-Asia.

Effects of habitat parameters on the faunal composition of communities

NESS(m_{max}=*10*)-indices of faunal similarity from sampling sites in Borneo were used to display the similarity of sites as proximity in a MDS-plot. Figure 3.4 shows a 2-dimensional MDS for easier graphic display, while a 3-dimensional MDS with lower Stress-values was

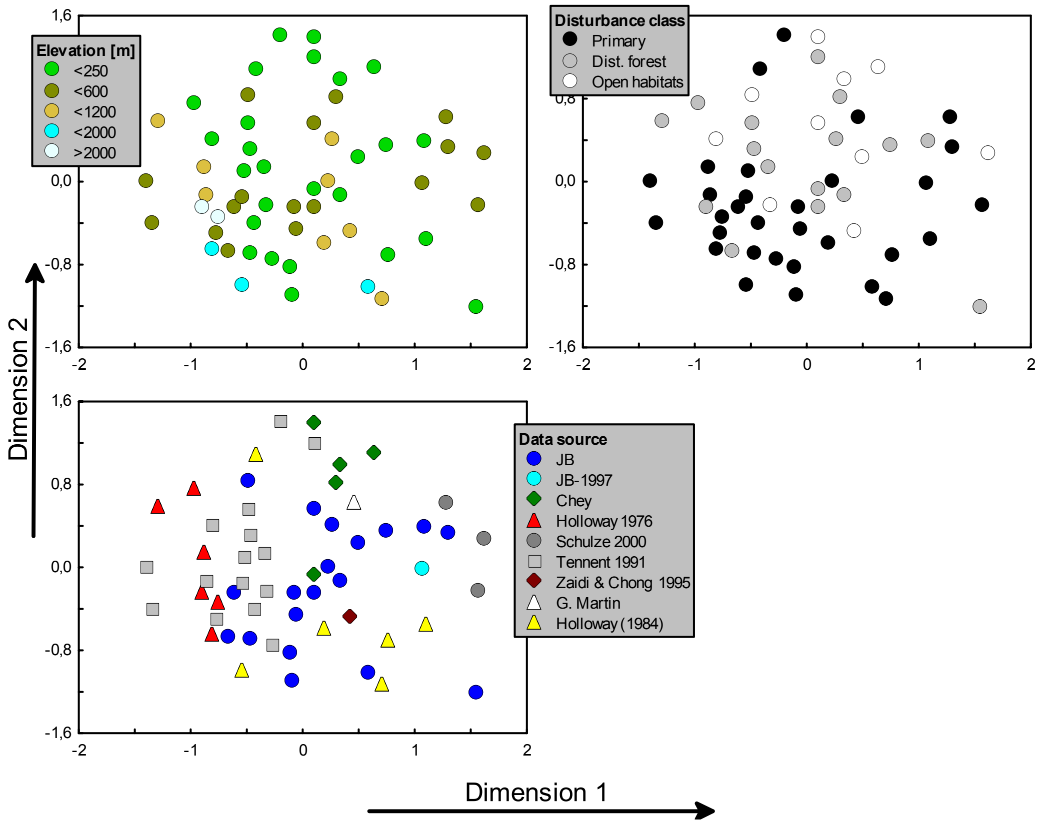


Figure 3.4 shows 2-dimensional non-metric MDS-plots for 57 Bornean sampling sites (Stress=0,237), displaying differences in elevation, habitat disturbance and data source.

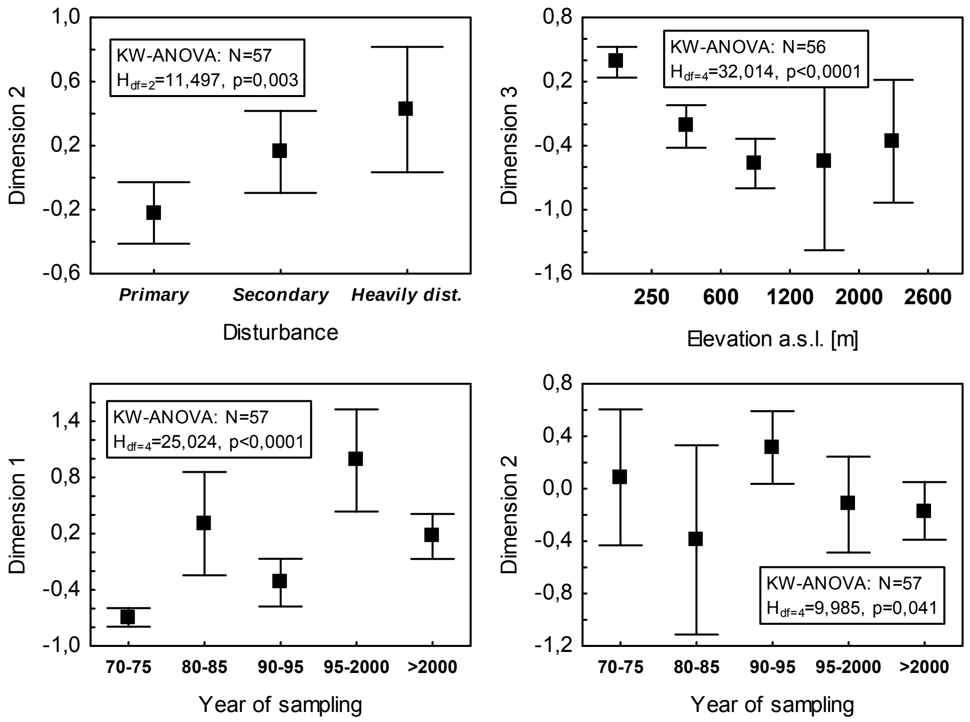


Figure 3.5 shows mean dimension values (±95%CI) from a 3-dimensional MDS-plot for 57 sampling sites on Borneo. Sites were grouped by disturbance, elevation class and half-decade of sampling year (see text). Univariate non-parametric tests are given in the graph (see text). The suspected univariate effect of 'full night'-sampling (not shown in figure, see table 2) on dimension 1 could not be confirmed (Mann-Whitney U-test: U=297, Z=-0,927, p=0,354), while it is significant on dimension 3 (U=150, Z=3,451, p<0,001).

used for further analyses (Stress=0,145, a Shepard diagram did not reveal deviations from general assumptions of the model, Cox & Cox 1994). Preliminary analyses identified three potentially influential variables (see figure 3.4): Moderate effects of habitat disturbance and elevation and – unexpectedly – a strong effect of the source of the data. As 'data source' is not a satisfying natural variable, a 'Generalized Linear Model' (GLM: Guisan et al. 2002, StatSoft 2003) was used to identify how values of the three MDS-dimensions are influenced by the potentially important parameters disturbance, elevation, sampling procedure (full night *vs.* not full night; see chapter 2), light source (mercury-vapour, blacklight, kerosene lamp) and 'half-decade of sampling year' (assuming that data were collected 1-2 years prior to publication if not otherwise stated). All suspected parameters except 'lamp type' have a significant influence on MDS-values in the multivariate design (table 3.2), and several direct influences on dimension values are suggested from univariate tests. However, MDS-values are ordination measures and do not reflect site similarity as interval-scaled data (Cox & Cox 1994). To exclude the chance that GLM analysis leads to misinterpretations of results even though general assumptions of data (Guisan et al. 2002) were fulfilled, non-parametric univariate tests (see also Seaman & Jaeger 1990, Stuart-Oaten 1995) were applied to data, which largely confirmed previous results (see figure 3.5 for details): Habitat disturbance is influencing dimension 2, whereas altitude of the sampling site has an effect on dimension 3 of the MDS. Of the 'data source'-related parameters, the 'year of sampling' is influencing dimension 1, but also has an effect on dimension 2 (the 'disturbance-axis'). While the effect of ‘full night’-sampling on dimension 1 is not confirmed in nonparametric tests (see figure 3.5), its influence on dimension 3 (the ‘altitude-axis’) is significant but likely to be a result of collinearity: Low values on dimension 3, which tend to be from higher altitudes, are associated with incomplete sampling nights. To further confirm that the effect of disturbance is not an artefact of the data source (e.g. *via* year of sampling), a GLM was used to analyses MDS-data based only on own sampling on Borneo (18 sites, always full night sampling, sampled between 2001 and 2003). The model is significant only for dimension 2 of three dimensions (R^2=0,433, F=3,563, p=0,042), which is based solely on the effect of habitat disturbance (univariate test: F=4,994, p=0,023).

	Multivariate significance test:			Univariate results:					
				Dim1:		**Dim2:**		**Dim3:**	
	1-Wilks λ	**$F_{df=3}$**	**p**	**$F_{df=1}$**	**p**	**$F_{df=1}$**	**p**	**$F_{df=1}$**	**p**
Elevation	**0,304**	**7,147**	**0,0004**	0,663	0,4191	3,783	0,0573	**13,707**	**0,0005**
Disturbance	**0,205**	**4,210**	**0,0100**	2,808	0,0999	**11,319**	**0,0015**	0,722	0,3993
Sampling year	**0,407**	**11,218**	**<0,0001**	**23,757**	**<0,0001**	**6,599**	**0,0132**	0,192	0,6629
Lamp type	0,024	0,407	0,7487	0,428	0,5158	0,298	0,5878	0,245	0,6225
Full night	**0,383**	**10,148**	**<0,0001**	**22,387**	**<0,0001**	1,151	0,2883	**4,161**	**0,0466**
Constant	0,398	10,782	<0,0001	22,999	<0,0001	6,173	0,0163	0,201	0,6562

Table 3.2 shows results for a Generalized Linear Model (GLM; StatSoft 2003), analysing potentially influential factors on dimension-values of a MDS. The model is significant for all three dimensions (Dim1: $R^2_{multiple}$= 0,418, $F_{df=5}$= 7,321, p<0,0001; Dim2: $R^2_{multiple}$=0,333, $F_{df=5}$=5,103, p<0,001; Dim3: $R^2_{multiple}$=0,396, $F_{df=5}$=6,695, p<0,0001). Multivariate significance tests identify all suspected factors except ‘lamp type’ as influential (1-Wilks λ can be interpreted as a measure of explained variance, analogous to R^2 in univariate tests; StatSoft 2003). Significant effects (bold print) in univariate tests suggest influences of a factor on respective dimensions (see also figure 5).

Effects of habitat parameters on the relative abundance of subfamilies

Sphingid subfamilies have been reported to differ in their life histories and vary in relative abundance under different conditions of disturbance and elevation (Holloway 1987a). Across 93 sites from Southeast-Asia, relative abundances of three subfamilies (as *specimens/total catch*) were compared for effects of disturbance class, elevation and geographic position (latitude/longitude) with a GLM. Results (table 3.3) indicate that only disturbance has a significant effect on subfamily frequency, while trends (p<0,10) for an influence of elevation and latitude were found (see also chapter 4.1). Univariate tests indicate an effect of latitude on Sphinginae-frequency and effects of disturbance on Smerinthinae and Macroglossinae frequencies. GLM’s are flexible to deviations of data from normality (Guisan et al. 2002), which some

	1-Wilks λ	**F**	**df**	**p**
Latitude	0,062	2,467	2	0,092
Longitude	0,017	0,654	2	0,523
Elevation	0,065	2,571	2	0,083
Disturbance	**0,179**	**3,828**	**4**	**0,005**
Constant	0,077	3,079	2	0,052

Table 3.3 shows multiple significance tests of influential parameters in a Generalized Linear Model (GLM; StatSoft 2003) on the proportion of Sphingid subfamilies in 93 samples in Southeast-Asia. The model gives significant predictions for Sphinginae ($R^2_{multiple}$=0,143, $F_{df=5}$=2,509, p=0,037) and Smerinthinae ($R^2_{multiple}$=0,156, $F_{df=5}$=2,767, p=0,024), while it is (barely) non-significant for Macroglossinae ($R^2_{multiple}$=0,120, $F_{df=5}$=2,046, p=0,082).

variables exhibited (KS-test: p<0,01). Furthermore, results were confirmed by non-parametric univariate tests (see figure 3.6). Similar analyses of Borneo-data alone (not shown) produced no significant multivariate results, but univariate trends along the same patterns (for elevation and disturbance). Similarly, analyses of relative species richness of subfamilies (as *species/total species richness*) have no significant results, but follow the same pattern as specimen frequencies. The subfamily frequency changes with increasing longitude (less Smerinthinae, more Macroglossinae) are not significant, but their direction matches results of an analysis of island faunas across the region (see chapter 4.1).

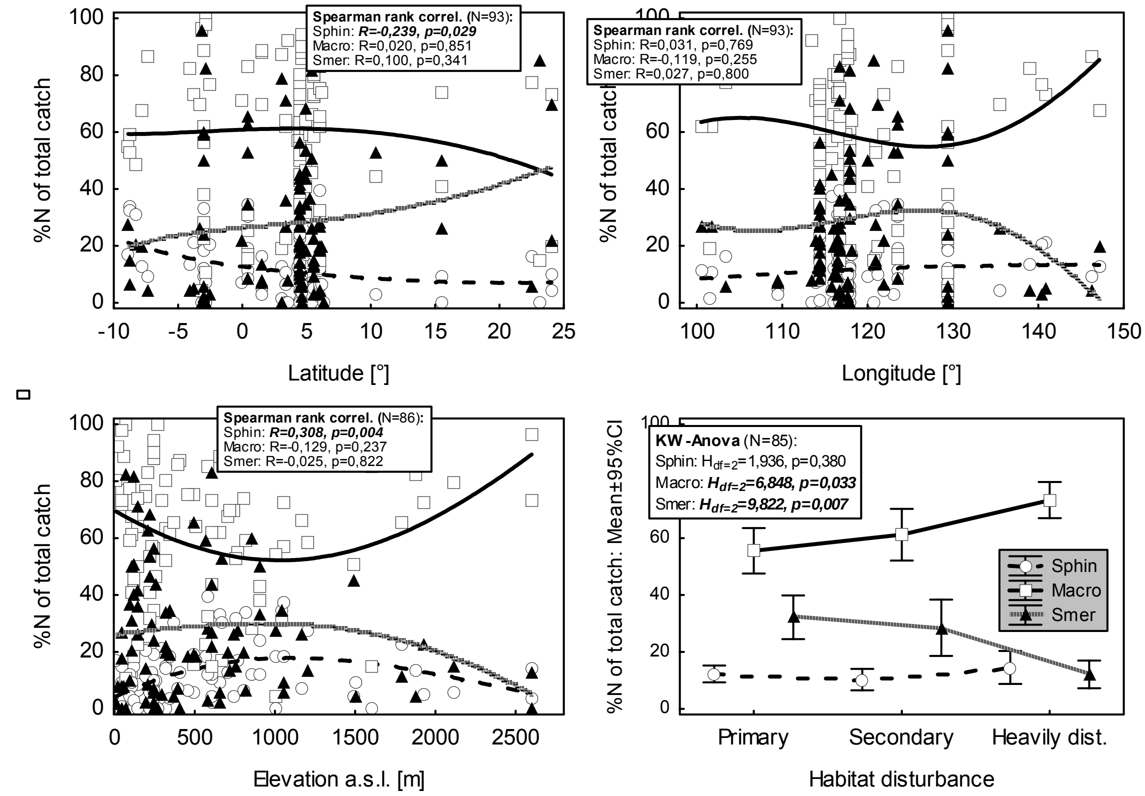


Figure 3.6 shows the influence of geographic position, elevation and habitat disturbance on the relative abundance of subfamilies in 93 local light catches across Southeast-Asia. Non-parametric univariate test values are given in the graphs; for a multivariate analysis see table 3. Negative exponential least square curves were fitted for display of trends, but do not infer statistical significance.

Turnover and geographic autocorrelation

The similarity of samples from Borneo (measured by NESS($m_{\max}=10$)) were tested for geographic autocorrelation, using the computer program *IBD 1.5* (Bohonak 2002). Geographic distances of sample sites were retrieved from latitude/longitude data (applying geodesic correction) with *Animal Movement Program 2.0* (Hooge et al. 1999), an extension for the GIS program *ArcView 3.2* (2000). Due to the original data entry of site coordinates with an error margin of ±30’ or less, a maximum measurement error of ca. ±80 km is possible. Distance has a significant effect on the community structure of sites (Mantel statistic, 1000 randomizations: Z=314,7 x 10^6, R=0,147, $p_{(\text{one-sided})}$ $\leq$0,012; see e.g. Manly 1997). To make sure that geographic autocorrelation is not an artefact of a correlation between distance and the data source (and connected variables, see above), only own sampling data from Borneo (18 sites) were also tested, which confirmed results on a lower level of significance (Mantel statistic, 1000 randomizations: Z=14,0 x 10^6, R=0,2097, $p_{(one-sided)}$ ≤0,035).

Figure 3.7 shows species turnover in relation to distance between sampling sites. Samples across Southeast-Asia exhibit a triangle shape which is expected due to biogeographic effects (chapter 4): Certain species cannot be found at distant sampling sites because they do not occur in the respective regions any more. This effect disappears if only Borneo-data are plotted, but the relation is still significant (see results from the Mantel-test above) if quantitative data are used. For presence/absence-based Sørensen indices turnover is not influenced by distance within the biogeographically homogenous island Borneo (data not shown). This confirms an assumption in Hubbell's (2001) 'unified neutral theory of biodiversity and biogeography': Within a 'metacommunity', where every species could reach every site, 'local communities' are influenced by the geographic autocorrelation of species' abundance which lets most 'rare species' appear over-proportionally rare on most sites (see chapter 3.2 for further discussion).

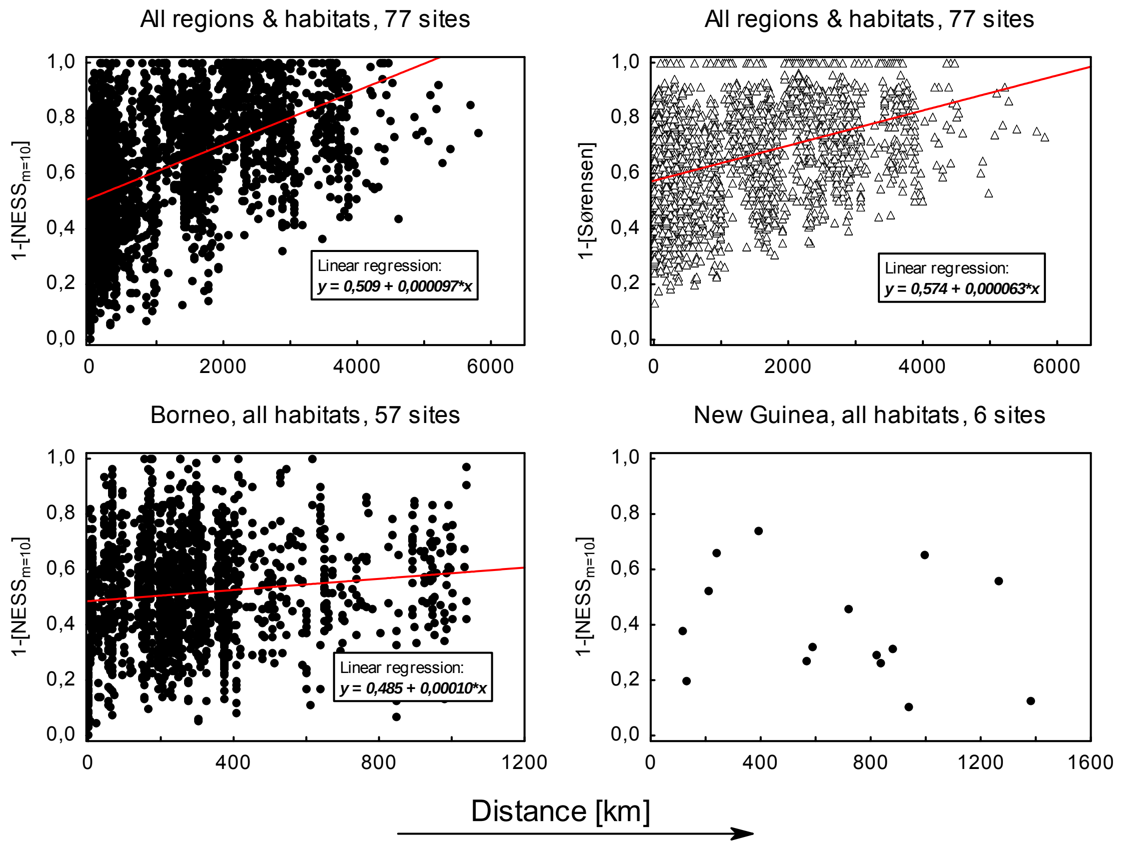


Figure 3.7 shows plots of distance and between-habitat diversity (as 1-similarity). The two upper figures include sample sites across Southeast-Asia (data from Sulawesi & Seram are not included, hence reduced sample size of 77 sites) and reflect biogeographic effects (triangle shape of data). Quantitative data (left upper graph) as well as presence-absence data (right upper graph) indicate an increase in faunal diversity with increasing distance. Within Borneo (left lower graph) data exhibits a weaker relationship which breaks down if only presence-absence data is considered (not shown). No relationship was found for New Guinea data (left lower graph), where sample size was considerably lower yet sites spanned a large altitudinal gradient. Statistical tests cannot be applied as this presentation inflates sample size with non-independent data, but Mantel statistics (see text) confirm the significance of the relationships.

Species turnover within more homogenous habitats (figure 3.8) indicates a steeper relation in lowland disturbed habitats than in forests of similar altitude, while no conclusion can be reached for montane regions.

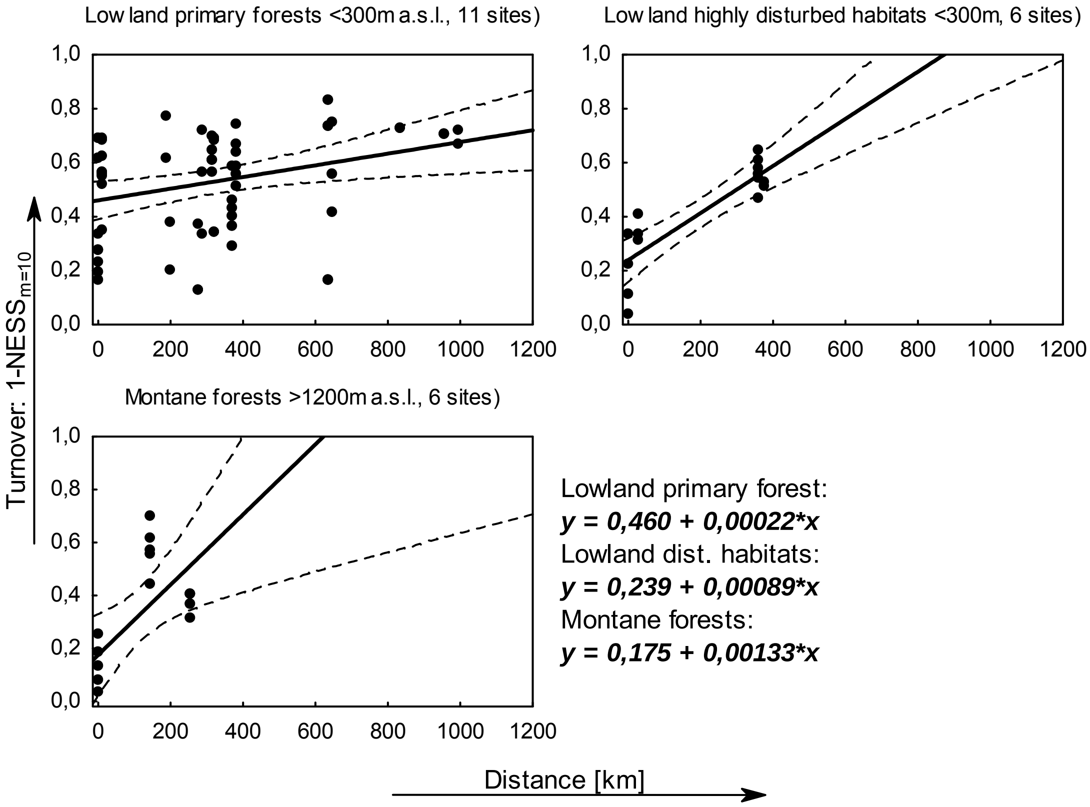


Figure 3.8 shows the relationship between distances and between-habitat diversity for selected habitats within Borneo. The steep regression slope of the lowland disturbed sites (upper right graph) is not an artefact of low sample size, a regression with all disturbed sites <600m a.s.l. has exactly the same slope (not shown). However, statistical tests (including 95% confidence bands of linear regressions) do not strictly apply, as this presentation inflates sample sizes with non-independent data.

Discussion

Habitat disturbance, altitude and life history traits

No influence of habitat disturbance on the within-habitat diversity of hawkmoths in Borneo was found, which confirms the conclusion of Schulze & Fiedler (2003b) on a considerably larger data set. Furthermore, among data from other regions, albeit on a smaller number of sites, no trends of any influence of disturbance were found as well. This result is in striking contrast to the reaction of a number of other Lepidoptera groups (e.g. Nymphalidae, Geometridae, Pyralidae; Hamer & Hill 2000, Beck et al. 2002, Fiedler & Schulze 2004, Beck & Schulze 2000), which decrease considerably in diversity at sites of high anthropogenic habitat disturbance. However, when taking a closer look at the data it became evident that taxonomic subgroups within the Sphingidae do react to habitat disturbance, but seem to compensate each others effect with regard to total diversity: The frequency of Smerinthinae specimens (and species) decreases with disturbance, while that of Macroglossinae increases. Generally, it must be expected that the ecological similarity of species, and therefore their habitat choice, is correlated with their phylogeny (Webb et al. 2002, Webb 2000), so effects of habitat parameters on higher taxon frequency are not surprising. Many Smerinthinae species (i.e., the tribus Smerinthini) have a reduced, non-functional proboscis which does not allow adult feeding (Lemaire & Minet 1998, Kitching & Cadiou 2000). This implies a *capital breeding* life-history where only larval resources are used for egg production and adult energy expenditure, which can have significant impacts on ecological characteristics of Lepidoptera species (Tammaru & Haukioja 1996). Presumably associated with this life history are a shorter adult life span and greater sexual dimorphism (see e.g. Janzen 1984). Macroglossinae, on the other hand, have a well developed proboscis (hence the name of the group, e.g. Miller 1997). Their *income breeding* life history implies that adult resources are used for reproduction and body maintenance, potentially resulting in longer adult life and associated features (Janzen 1984, see also Kaitala et al. 2002). For Sphinginae, which share similar life history traits as Macroglossinae, no changes of their generally low frequency were observed. Smerinthinae might be suspected to be less efficient dispersers due to their (presumed) shorter adult life-span or lower flight abilities (see also chapters 4.1 & 5.2) although no evidence for this was found within Borneo (Schulze 2000). Still, data indicate the trend that the partly *capital breeding* Smerinthinae are better adapted to stable primary habitats, while *income breeding* Macroglossinae thrive in disturbed sites, which probably were mostly ephemeral before the recent period of massive anthropogenic habitat conversion in the Indo-Australian tropics (Bowles et al. 1998, Sodhi et al. 2004). For further support of the idea that life history influences responses of taxa to habitat parameters, see box 3.1. However, this hypothesis is weakened by the Smerinthinae-tribus Ambulycini, which are adult feeders (see chapter 1.2) yet exhibit the same reactions to habitat disturbance as (confirmed non-feeding) Smerinthini (not shown). In Bornean local assemblages Ambulycini and Smerinthini contribute approximately equally to the total species and specimen numbers. More knowledge about the natural history of the Ambulycini is needed to understand the biodiversity reactions of this group, as will be further discussed in chapter 7.

Faunal composition of Sphingid assemblages on Borneo is significantly influenced by habitat disturbance (see e.g. figure 3.5). This finding is in contrast to results from Schulze & Fiedler (2003b) who found no influence of disturbance on Sphingid β-diversity despite similar analysis techniques (i.e. NESS-index, non-metric MDS). Two differences between Schulze & Fielder (2003b) and this study might be responsible for this difference: A large sample size might have made it possible to find community changes that were not visible at smaller sample sizes. Furthermore, the classification of habitat disturbance differed between the studies: While Schulze & Fiedler (2003b) dichotomously compared strictly primary habitat with habitats of any degree of disturbance, this study was (due to a large sample size) able to classify habitats by also differentiating between secondary, degenerated forests and heavily disturbed, open landscapes. Several studies on Lepidoptera diversity indicated that this stage of habitat conversion might create the greater change in communities than a primary forest to secondary forest conversion (e.g. Willott 1999, Willott et al. 2000, Schulze 2000, Beck et al. 2002).

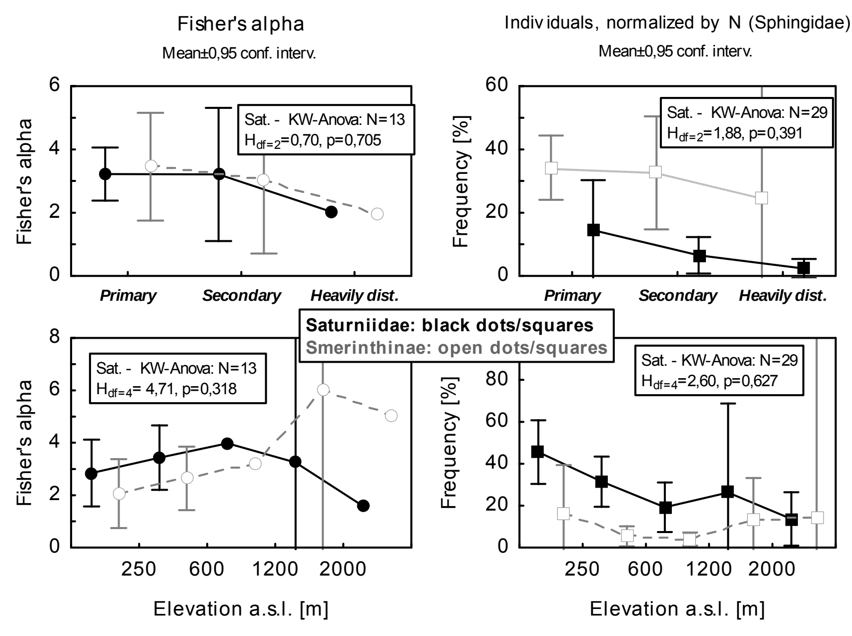
Most studies on habitat disturbance investigate a gradient (e.g. Schulze & Fielder 2003a, Beck et al. 2002) or differently disturbed sites (e.g. Willott 1999) in close proximity to each other, which avoids the influence of biogeographical or regional differences in species composition. Data in this study, however, were compiled from different sources, times and regions, and are therefore less controlled for additional influences besides the 'target' variables (i.e., habitat disturbance), which probably 'blurs' effects to a certain degree. Multivariate analysis becomes necessary to filter out relevant effects and sometimes leaves some doubt if the right parameters of a large number of possibilities were chosen (see also McNally 2000). The resulting large sample sizes, on the other hand, allow results and conclusions on a larger regional scale, as (at least on Borneo) all major habitat types were covered by data. It was

Box 3.1: Diversity patterns of the Saturniidae

The family Saturniidae shares similarities in life-history with many species of the Sphingid subfamily Smerinthinae. Both groups have non-feeding adults, as opposed to the Sphingid subfamilies Sphinginae & Macroglossinae. Janzen (1984) elaborately discussed consequences of life history differences between *income breeders* and *capital breeders* in tropical big moths in the neotropics, where Saturniidae are very species-rich while Smerinthinae are rare. Holloway (1987) suggested that Smerinthinae in Southeast-Asia 'fill' the position of missing Saturniid species in several ecological aspects.

At sampling sites in Borneo, Saturniidae were recorded if they came to light. Determination is preliminary in some taxa of the genus *Antherea*, where specimens were counted as the most likely taxa (from Holloway 1987) for this analysis, while they might actually prove to be new taxa. Furthermore, data from Holloway (1976) and Holloway (pers. com., see also 1984) were included in this analysis. The generally low abundance of Saturniidae led to a relatively small sample, but for 17 sites in Borneo patterns of diversity and relative family abundance can be compared (N=314, S_{prelim}=19).

The graph below shows patterns for the within-habitat diversity (as Fisher's α) and relative abundance (normalized by total Sphingidae catch) along gradients of disturbance- and elevation-classes. The data for Smerinthinae from the same sampling sites are shown for comparison.



No statistically significant effects could be found, but reactions to environmental gradients seem to be similar between the two taxonomic groups, particularly with reference to habitat disturbance. The decline in relative abundance with increasing disturbance is in marked contrast to *income-breeding* Macroglossinae (see fig. 3.6).

tried to confirm results with a *Canonical Correspondence Analysis* (CCA), but this alternative method of ordination performed poor in both explaining the original variance of data (16%) as well as assigning the 4 environmental factors to axes, supporting Brehm & Fiedler's (2004) judgement of MDS as superior ordination technique.

In preliminary analyses 'data source' proved to be the most influential predictor of community composition. This is an important call for careful analysis of multi-source data, but it is a very unsatisfying result if one looks for biologically relevant habitat parameters. Data sources not only varied in methodological aspects (light source, schedule of nightly sampling), but also in sampling regions within Borneo (which differ due to geographic autocorrelation of communities, see above, or floristic composition, see e.g. Slik et al. 2003 for trees), the year of sampling, altitudinal zone and habitat type (e.g., Chey 1994 sampled almost exclusively on lowland softwood plantations in the south-east of Sabah). The parameters which were finally chosen for analysis (see table 3.2) could all be reasonably expected to cover a portion of the 'data source'-variability (e.g. chapter 2) and succeeded in a significant multivariate model which filtered out effects that are readily interpretable: Elevation and habitat disturbance are major environmental parameters that influence almost all investigated biological communities (e.g. McCoy 1990, Lawton et al. 1998, Huston 1994). The sampling schedule (full night *vs.* part of the night) was already *a priori* expected to influence samples (chapter 2), whereas the influence of the year of sampling is an unexpected, yet possibly important and interpretable finding (see below). However, it should not be forgotten that at least some of these parameters could co-vary with yet unknown variables that influence Sphingid assemblages, but are still hidden in the variation of 'data sources' (McNally 2000, see also Oliver et al. 2000).

Elevation was found to be a significant predictor of faunal assemblages (figure 3.5). However, no statistically significant trends of their within-habitat diversity were found, although plots suggest a mid-elevational peak over 1000 metres a.s.l. both for Borneo (figure 3.2) as well as for pooled data from Southeast-Asia (data not shown). While the biodiversity of many taxa is generally decreasing with increasing altitude in the Indo-Australian tropics (e.g. McCoy 1990, Lakim et al. 1999, Biun 1999, Brühl et al. 1998, Häuser et al. 1997, Hebert 1980, Wolda 1987, Mey & Speidel 2003, Robinson & Tuck 1993), a mid-elevational peak is found for many Lepidoptera groups (Holloway 1993b, Holloway et al. 1990). Reasons for this 'thousand-metre bump' (Holloway 1987b) might be an overlap of lowland and montane fauna (e.g. Schulze 2000, Holloway & Nielsen 1999, Pyrcz & Wojtusiak 2002), Pleistocene extinctions in the lowlands (Holloway et al. 1990, Holloway & Nielsen 1999), or high speciation rates in montane regions (as e.g. in the butterfly genus *Delias*, Parsons 1999, H. v. Mastrigt pers. com.). Furthermore, such altitude patterns were associated with the mid-domain effect (Colwell & Lees 2000) in other taxa (e.g. McCain 2004, Bachman et al. 2004, Grytnes & Vetaas 2002, but see Zapata et al. 2003 for a general critique of this hypothesis). Schulze (2000) found a mid-elevational peaks for recorded Sphingid species richness on an altitudinal gradient in Kinabalu Park in north-eastern Borneo (most data from higher elevations on Borneo stem from Mt. Kinabalu, which is the highest and best-surveyed mountain on the island; see e.g. Schulze et al. 2000, Kitayama 1992, Wong & Phillips 1996). Furthermore, he reports a similar taxonomic dichotomy as it was found for habitat disturbance (see above): Macroglossinae (and to a lesser degree Sphinginae) are species-rich from the lowland up to the lower montane region, while Smerinthinae are relatively species-poor in the lowland and exhibit a strong rise in recorded species with increasing altitude and reach a peak in the lower montane forest. Both groups show a sharp decline in species richness above 1600 metres altitude. Data in this study (not shown) confirm the reported patterns (Schulze 2000) for the species diversity of subfamilies (as Fisher's α) for Borneo, while the normalization for total catch size in figure 3.6 hides the general decline in specimens, species and diversity at high altitudes.

A *capital breeding* life history might be connected to larval food plant choice (Schulze 2000, Miller 1997) and should lead to the use of stable resources due to limited dispersal abilities (see above with reference to habitat disturbance). Trees are a more stable resource than herbaceous plants and are more commonly taken by Smerinthinae caterpillars than by other subfamilies (Holloway 1987a). However, the dominating tree family Dipterocarpaceae in Southeast-Asian lowland forests (Whitmore 1990) is rarely taken by Sphingidae caterpillars, although it is recorded as a host plant for *Cypa decolor*, *Ambulyx canescens* and *A. substrigilis* (see also chapter 5.1). All three species belong to the Smerinthinae, the latter two are relatively common in lowland primary forest. It has been argued (Schulze 2000) that Smerinthinae might be more divers in montane regions because suitably stable larval resources might be more abundant there due to a change in plant family composition (e.g. Gentry 1988) and a generally lower tree diversity in montane forests (e.g. Kitayama 1992), which diminishes the time to find a specific resource.

Both habitat parameters (altitude and disturbance) influence the large Sphingid subfamilies Macroglossinae and Smerinthinae differently, while Sphinginae show no reaction (or are just too few to observe trends). An idealised picture of Smerinthinae as bad dispersing, stable-habitat specialists and Macroglossinae as well dispersing, disturbed-habitat preferring taxon emerges, which will be further discussed with results from biogeography analyses (chapter 4.1).

Effects of sampling year on Sphingid assemblages: climate, habitat conversion or just 'noise'?

The year of sampling (measured in half-decades) emerged as an influential predictor of Sphingid assemblage composition. If this is not an artefact of an unknown, co-varying parameter of 'data source' (see above), it is an unexpected yet relevant indication of long-term change of a tropical insect community. During three years of own sampling no effects of seasonality were observed in re-sampled sites (chapter 2), but species assemblages changed slightly between re-samples. Thus, seasonal effects, which were observed on insect taxa in other tropical regions (Novotny & Basset 1998, Intachat et al. 2001, Wolda 1978), can probably be excluded as reason for the observed changes for hawkmoths in Borneo (see also Barlow & Woiwod 1993, Hebert 1980, Novotny et al. 2002b). Long-term changes of Southeast-Asian hawkmoth assemblages are quantitatively documented here for the first time, but were also observed by collectors who regularly sampled at the same sites for decades (e.g. H. Barlow pers. com, H. v. Mastrigt pers. com.).

Long-term temporal changes of biological communities are not an unusual phenomenon, but are mostly well-documented only for plants and vertebrate taxa from temperate regions or for taxa with special relevance, such as game or pest species (see e.g. Rosenzweig 1995, Maurer 1999, Lawton 2000 for manifold examples & references). Population fluctuations of species can be regular or synchronized by an outside factor (see Selas et al. 2004, Bjørnstad et al. 1998 for examples on moths), or they can be irregular, temporally autocorrelated (‘red noise’) or completely random (‘white noise’; Lawton 2000, Akçakaya et al. 2003). Obviously, even with huge amounts of data it is very difficult to separate the latter from the former (Lawton 2000). Leaving aside the possibility of an artefact result due to multicollinearity of predictor variables (McNally 2000, see above for discussion), two potentially influential factors on temporal changes of hawkmoths assemblages in Borneo come to mind: Deviations from the otherwise very stable and uniform climate during the irregular ‘*el-niño* southern oscillations’ (e.g. Kitayama et al. 1999), a weather phenomenon that leads to several months of draught every few years and that has potentially far-reaching biological impacts (on trees: Slik 2004, Wich & van Schaik 2000, on butterflies: Cleary & Mooers 2004, Itioka & Yamauti 2004, but see Hill et al. 2003). Furthermore, a rapid large-scale habitat conversion has changed Borneo (as well as many other tropical rainforests, Bowles et al. 1998, Sodhi et al. 2004), which until the beginning of industrial logging in the 1950’s (Marsh et al. 1996) was mostly covered with relatively undisturbed forest.

El-niño years since 1970 were identified in 1973, 1978, 1983, 1987, 1991-95, 1997-98 and 2002 (source: *http://www.elnino.noaa.govT*). Thus, *el-niño* climate changes occurred in all of the analysed sampling periods (in 5-year steps) and cannot be associated with the observed Sphingid community changes at this temporal resolution. However, the strongest *el-niño* events were identified in 1983 and 1998, which matches the highest values on dimension 1 of the MDS (figure 3.5) in the corresponding half-decades. Therefore, the idea that Sphingidae assemblages are influenced by this global climate phenomenon cannot be ruled out either. Temporal changes of the community are mostly projected on dimension 1 of the MDS-plot, but to a lesser degree also on dimension 2, the ‘disturbance axis’ (see figure 3.5). However, values seem to decrease rather than increase with time, thus developing towards ‘primary habitat’ – a counterintuitive result that might be explained by better accessibility of jungle regions in modern times, which allows easier sampling in primary habitats or by an increased interest in the ecology of primary habitats. In conclusion, no proof for an influence of the large-scale habitat conversion on Borneo on local samples of hawkmoths over the course of the least 30 years could be found in the data.

Species turnover, anthropogenic habitat homogenization, and estimates of regional richness

One of the suspected threats of anthropogenic habitat conversion in tropical regions is ‘habitat homogenization’ (McKinney & Lockwood 1999, see also Collins et al. 2002 for recent discussion), the conversion of rainforest sites with high between-habitat diversity into homogenous cultivated areas. It is expected that disturbed sites are to a larger proportion populated by opportunistic species which are adapted to reach such regions quickly (e.g. Kitahara & Fujii 1994, see also discussion of differences between subfamily-responses to disturbance). This idea can be tested by predictions for the distance-turnover relation for Bornean Sphingidae: Primary forest samples should exhibit a steeper turnover than heavily disturbed sites. As figure 3.8 shows, the opposite is found in data: Species turnover appears steeper for disturbed lowland sites than for lowland primary forests. Other studies on Lepidoptera in Borneo (Geometridae: Beck et al. 2002, Nymphalidae: Schulze, Beck, Brühl et al., *unpublished*) also failed to find evidence of the 'homogenization hypothesis', as habitat disturbance had no influence on the magnitude of differences between regions.

Montane habitats are often considered as relatively isolated 'habitat islands' in tropical landscapes (e.g. Bowers 1988) and frequently contain a number endemic species (see e.g. Wong & Phillips 1996 for Mt. Kinabalu). Mountain peaks might thus be expected to exhibit a stronger species turnover than (connected) lowland sites. However, this assumption might or might not be true as (a) Sphingidae are probably easily able to reach mountain peaks within Borneo, and (b) montane regions are quite common in northern and central Borneo. Figure 3.8 tentatively supports the prediction by a trend to high turnover in montane habitats (>1200 metres a.s.l.), but the number of available sample sites is too low for reliable regression fitting.

Estimating regional species richness from local samples

Sphingidae were exhaustively sampled at least in Northern, non-Indonesian Borneo, which is one of the best-covered regions for this taxon in the Indo-Australian tropics. Despite a significant geographic autocorrelation of quantitative samples (see above), β-diversity between regions on the island is apparently not very high: Schulze et al. (2000) record two thirds of the known species from Kinabalu Park (as similar proportion was found for butterflies and primates, Häuser et al. 1997, Schulze & Beck 1999). Even although this figures might be misleading as (1) Kinabalu Park is an exceptionally divers region due to its unmatched altitudinal range and (2) the park is by far the best-sampled region of the island (see above for references), there is not much indication that Borneo's Sphingidae fauna is not (almost) completely known. This gives the unique possibility to compare a large data set of short, intense samples

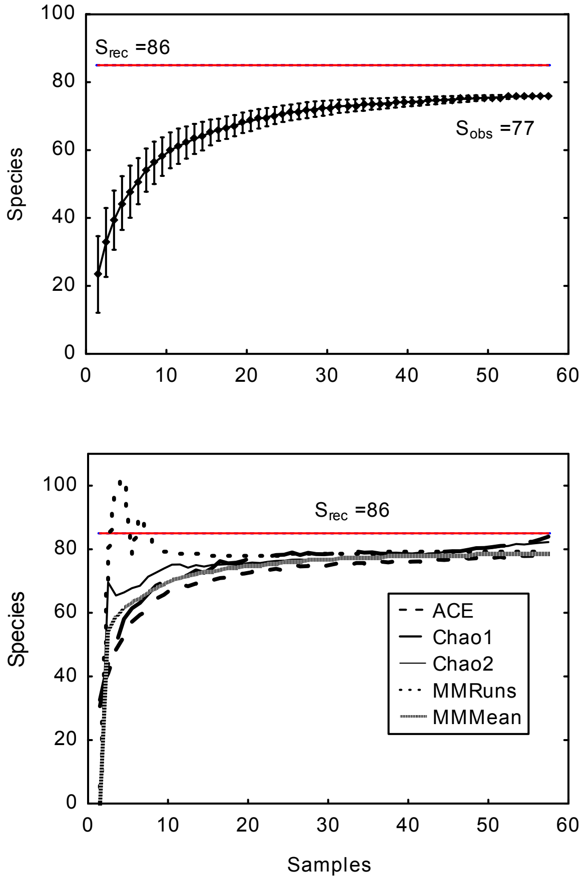


Figure 3.9 shows 100-fold randomised species accumulation curve [±SD] (upper figure) and estimators of 'true' species richness (lower figure) from 57 quantitative local samples on Borneo. Randomisations and calculations of richness estimators were executed with *EstimateS 5.01* (Colwell 2000). Total known species richness for Borneo was taken from the Checklist in Beck & Kitching (2004), excluding species of the genera *Macroglossum*, *Cephonodes* & *Sataspes*, which are day-active and can only rarely be caught at light.

with a relatively complete inventory of 125 years of sampling for this insect taxon (see Checklist in Beck & Kitching 2004). Hammond (1994) suggested using local samples for extrapolation to regional species richness for less well-known groups (see also Mawdsley 1996, Novotny & Missa 2000, Krishnamani et al. 2004). Figure 3.9 shows species accumulation curves (see e.g. Leon-Cortez et al. 1998, Moreno & Halffter 2000, Willott 2001) and estimators of 'true' species richness (Colwell & Coddington 1994, Colwell 2000) of quantitative data. Both measures reach stable, apparently reliable values at 20-30 local samples, but miss the total known species richness of the island by ca. 10%. Some recently recorded species on Borneo might still be restricted to the regions of their initial invasion on the island (e.g. *Daphnis nerii*, see Beck & Kitching 2004), but quantitative sampling still underestimates regional richness slightly. Considering (1) that it will rarely be possible to use such a comprehensive set of sampling sites for analysis, (2) that Sphingidae are a relatively species-poor taxon of insects in tropical rainforest regions, and (3) that their β-diversity and geographic autocorrelation of faunal composition is probably comparatively low due to their high dispersal abilities (chapter 4), estimates of regional species richness from local samples must probably generally be corrected upwards to an unknown extent (see also Ugland et al. 2003 for an alternative model of fitting species-accumulation data, Petersen & Meier 2003, Petersen et al. 2003 for similar results on European Diptera).

The relationship between local and regional species richness

Phytophagous insects seem to form non-interactive local communities more often than strongly interactive (e.g. competition structured) ones (Strong et al. 1984, Cornell & Lawton 1992, but see Denno et al. 1995). In such communities without much biotic interaction, theoretical 'niche space' is available in excess, and communities are not 'saturated' with regard to species richness: The number of locally present species (as well as their identity) is more dependent on the size and composition of the regionally available species pools (which is influenced by biogeographical processes) than on local ecological processes (Cornell & Lawton 1992, see also Shorrocks & Sevester 1995).

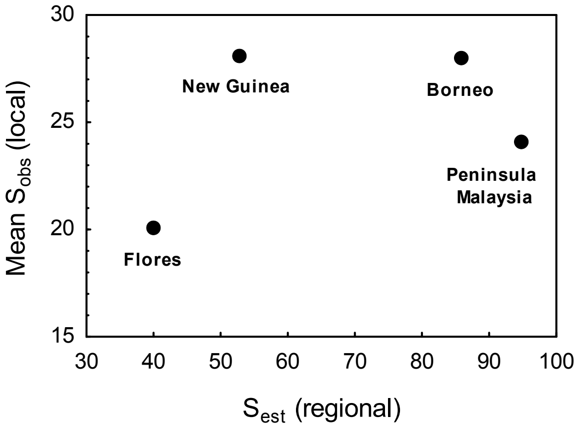


Figure 3.10 shows the relationship between estimated regional species richness (from Beck & Kitching 2004) and mean observed species richness from 26 local samples, using only forested sites below 1000 metres altitude. Only sites with more than 80 recorded specimens were used to calculate mean local species richness, day-active genera were excluded from local as well as regional data.

Plots of local *vs.* regional species richness can be a useful tool to assess if local species assemblages are saturated, or if the regionally available species pool determines local species richness (Srivastava 1999, see also Bell 2003). A linear relationship indicates the latter, while saturated communities do not exhibit any relationship or are better described by a curvilinear fit. However, this approach has recently been criticized (Mouquet et al. 2003), as the assembly time of a community, which depends on habitat size and fecundity of the species and is unknown for the taxa in this study, might be an important co-variable that influences this relationship. Regional species richness of Sphingidae was taken from estimated island checklists (Beck & Kitching 2004, see also chapter 4.1). Mean values of local richness for regions (islands) were used to avoid pseudoreplicates (Srivastava 1999), using only local samples of more than 80 specimens to attain a relatively high level of 'completeness' of observed species richness (see chapter 2). Furthermore, only relatively homogenous subsets of habitats were analysed (using only forested sites below 1000 metres a.s.l.). This procedure leaves only four regions for analysis, which makes statistics impossible: The power of the linear regression in figure 3.10 is <0,1 - already a power of 0,5 would require a sample size of 22 at the same effect size (computed with *GPower 2.0*, Faul & Erdfelder 1992). However, the distribution of data in figure 3.10 suggests no linear trend at all, but seems to approach a curvilinear fit as predicted for saturated communities (Cornell & Lawton 1992, Srivastava 1999). Inclusion of local samples with less than 80 individuals leads to increased sample size (adding data for the islands Negros, Lombok & Luzon), but does not increase the linearity of the relationship (neither for S_{obs} nor for Fisher's α as a measure of local diversity). It must be tentatively concluded that most Sphingid assemblages are saturated: Local species richness is determined by local ecological processes, not by the size of the available species pool (see also Novotny & Missa 2000 for Hemiptera and further references), a finding that is in contrast to analyses of tropical tree communities (Leigh et al. 2004, see also Ricklefs 2004). Average local richness is usually lower than most regional faunas (Mean±SD of species richness of the data in figure 3.10 is 27,5±8,6). However, some local samples exceed the regional species richness on some islands: For example, H. Barlow (pers. com.) collected 60 species in over 25 years of sampling at his house in Peninsular Malaysia. Furthermore, the decrease in local diversity with increasing longitude (see above) matches a decrease in the regional species richness (of island faunas) as one moves Southeast through the Malesian archipelago (see chapter 4).

CHAPTER 3.2 - RANK-ABUNDANCE DISTRIBUTIONS

Abstract

Species-abundance data of Sphingidae from 93 light-trapping samples across Southeast-Asia are well described by the *lognormal* distribution, which fits 98 percent of samples. The *logseries* distribution also does not deviate significantly from data in 94 percent of the samples. The *broken stick* distribution is considerably poorer in fitting the data: more than one third of samples deviate significantly from the model.

Rank-abundance distributions of regional (means per species) and local assemblages (means per rank) largely follow the patterns which are predicted by Hubbell's (2001) neutral model, although mean frequencies of species are significantly phylogeneticly autocorrelated – i.e., species are not ecologically neutral, but carry inherited traits that, to a certain extent, determine mean local abundance.

Data may contain a number of methodologically caused biases, such as using pooled data of heterogeneous assemblages, and assuming equal habitat productivity (of hawkmoths) across sampling sites. These potential weaknesses are thoroughly discussed to allow for an proper interpretation of results.

Introduction

The distribution of the relative abundance of species in local assemblages follows regularities that can be described by mathematical distribution models: If sorted by rank, species' frequencies tend to follow a 'hollow curve' (Robinson 1998, May 1975) with a few very abundant, some medium-abundant, and many rare species. This pattern is particularly obvious in species-rich samples (e.g. insects from the tropics), but is almost ubiquitous in its general trend (Hayek & Buzas 1997). Fisher et al. (1943) have successfully proposed the distribution model of the *logarithmic series* (empirically based on Lepidoptera catches in Southeast-Asia), of which the diversity index Fisher's α is derived (Kempton & Taylor 1974), while Preston (1948) alternatively proposed the *lognormal* distribution as a suitable description of the rank-abundance relationships. Frequency distributions are not only a pivotal point in the measurement of species diversity ('evenness' is basically a measure of this distribution, Weiher & Keddy 1999, see also Southwood & Henderson 2000), but may also give clues about the underlying mechanisms of community assemblage. Based on a model of niche partitioning, McArthur (1965) proposed the *broken stick* distribution, which has received little empirical support (Hubbell 2001), while the empirically derived *logseries* and *lognormal* distributions (May 1975, Tokeshi 1993) fit most samples of organisms that were ever taken. Many more phenomenologically or mechanistically derived distributions have been proposed since then to provide the 'best fit' to species abundance distributions (see e.g. Tokeshi 1993, Bell 2000, Plotkin et al. 2000, McGill 2003, Solé et al. 2004, Nummelin & Kaitala 2004).

The *logseries* was often viewed as the better-fitting distribution (e.g. Kempton & Taylor 1974), but recently available, very large samples are better described by the *lognormal* (see Hubbell 2001 for data and further references). Despite an apparent 'competition' between these two models, several attempts were made to show that both distributions might be 'special cases' of a general distribution model (e.g. Diserud & Engen 2000, Hubbell 2001). Attempts to derive the empirical distributions, including the skewed *lognormal* form in many very large data sets (Nee et al. 1991, Hubbell 2001), from biologically meaningful first principles (see also Basset et al. 1998) are increasingly successful for neutral models (e.g. Bell 2000). Hubbell (2001) proposed the *zero-sum multinomial* distribution (*zsm*) based on his neutral model of population growth, which derives *lognormal*-like patterns for local assemblages, while infinitely large samples of the 'metacommunity' (Hubbell 2001) yield a *logseries*-like distribution pattern (but see Alonso & McKane 2004, also McGill & Collins 2003, Bell 2000, Mouillot et al. 2000, Engen & Lande 1996a, b, Hengeveld & Stam 1978, Kempton & Taylor 1974, May 1975, Preston 1962a, b for alternative approaches). Despite the compilation of many supporting examples by Hubbell (2001), his model has so far received little independent empirical support (e.g. McGill 2003, Ulrich & Ollik 2004, Leigh et al. 2004).

In an empirical approach, comparisons of rank-abundance data with the 'standard models' of species-abundance relations can give important clues of the structuring of the assemblage under investigation (Southwood & Henderson 2000). Deviations from the models can give hints about the unusual ecology of species that cause the deviation. For example, plots of the rank abundance relationship of Geometrid moth samples from a traditionally cultivated region in Borneo identified several species which were clearly commoner than predicted by the model (see Beck et al. 2002). Three of these four species were found to be feeding on plants which were planted or otherwise promoted by human agriculture. Hill & Hamer (1998) suggested using species-abundance distribution as a measure of community change under different disturbance regimes, but methodological problems complicate this approach (e.g. Basset et al. 1998, Ghazoul 2002, see also Nummelin & Kaitala 2004).

The abundance of species can vary considerably under different ecological situations, temporally as well as spatially (e.g. Lawton 2000). Idealised, species are most abundant in the centre of their range, while they decline in frequency as they reach less suitable habitats towards the edge of their geographic distribution (e.g. McGill & Collins 2003). However, in reality they often exhibit a multi-peaked abundance distribution (Hengeveld 1990, Brewer & Gaston 2003), particularly in fragmented landscapes such as an island archipelago. Unlike in most model approaches, real landscapes can be a very scattered mosaic of suitable and unsuitable habitats for a given species, which certainly should influence its absolute and relative abundance (Schoener 1987). Still, certain biological characteristics can often be associated with 'rare' species (Kunin & Gaston 1997, Murray et al. 2002, Bruno 2002), and it is unclear to what degree rarity in an assemblage is determined by inherited traits. Particularly species-rich samples of tropical invertebrates often contain amazingly rare species (Magurran & Henderson 2004), which are frequently interpreted as 'tourists' out of their natural habitat (e.g. Ødegaard 2004, Novotny & Basset 2000, Schoener 1987).

Here, the frequency distributions of Sphingid moths from light-trapping samples in Southeast-Asia were used to investigate

(1) to what degree they fit standard models of rank-abundance distributions, and

(2) how frequency distributions of local and regional samples resemble the patterns predicted by Hubbell's neutral theory (2001).

(3) Furthermore, data of mean relative abundances of species were tested for phylogenetic autocorrelation (see e.g. Harvey & Pagel 1991, Garland et al. 1999 for reviews). A significant influence of phylogeny on the frequency would be a strong indication that the rarity and commonness of species has an inherited component.

Methods

Quantitative data from light-trapping stem from own collecting as well as a compilation of published and unpublished data from 93 sites across Southeast-Asia (see chapter 3.1, appendix I for details). The minimum number of specimen at a site were 20, data for day-active genera (e.g. *Macroglossum, Cephonodes & Sataspes*) were generally excluded. The majority of sites (57) are on Borneo, but samples cover most major regions from Vietnam to New Guinea.

Data were tested for goodness of fit to standard distribution models by χ^2-tests, comparing observed and expected abundance in octaves ($\log_2$-classes, see e.g. Hayek & Buzas 1997). Tests were performed with the computer program *Species diversity and richness 2.65* (Henderson & Seaby 2001). Expected frequencies for the *logseries*-distribution, which is displayed in several graphs, were taken from the 'Whittaker plot' of a fitted *logseries*, using the *Programs for Ecological Methodology* (Kenney & Krebs 1998).

To test for phylogenetic independence of the mean frequencies of species (as advocated e.g. by Webb et al. 2002), the randomization method of Abouheif (1999) was used. The *Test for Serial Independence* (Reefe & Abouheif 2003, see also Abouheif 1999) was applied to investigate the assumption of phylogenetic independence within the set of mean frequency data, i.e. to test whether species' frequencies are significantly associated with their phylogenetic history. Means of frequencies were calculated from all sites where a species was found, while the absence of a species at a site was not considered. An updated version of the systematics in Kitching & Cadiou (2000, I.J. Kitching, pers. com.) was used as a phylogeny-surrogate for Sphingidae, allowing for unresolved nodes where applicable. From 3000 randomizations of the original phylogeny (flipping of the nodes, which leaves the original structure intact yet changes neighbouring relationships of values), a mean 'observed value' of the *C-statistic* (derived from summed differences between successive values ordered by phylogeny; see Abouheif 1999 for details) was calculated, which is compared to the *C-statistic* of data from 3000 randomized phylogenies. Computations were executed with the program *Phylogenetic Independence 2.0* (Reefe & Abouheif 2003).

Results

Fit to standard models

Both the *logseries* as well as the *lognormal* distribution fit most observed data well (see table 3.4), while the broken stick distribution was much less suitable to describe rank abundance relations. Figure 3.11 shows examples of rank-abundance plots for sample sites with more than 800 specimens. The *lognormal* distribution fitted more local samples than the *logseries*. To assess which model had an overall better fit to the data, a meta-analysis (Scheiner & Gurevitch 2001, using the program *MetaWin 2.0*, Rosenberg et al. 2000) of the goodness-of-fit tests was conducted, using only the 64 sites for which tests both for the *logseries* and the *lognormal* model were available. The χ^2-values were first transformed into Pearson's r-values (Rosenberg et al. 2000), which were then used to calculate the effect size measure Fisher's z-transform (z_r). Meta-analysis summary showed lower effect sizes (i.e., better fit) for the *lognormal* (z_r±95%CI =0,066±0015) than for the *logseries* (z_r±95%CI =0,080±0,016), which were both significantly different from zero, but not significantly different from each other. Furthermore, there is no indication that effect size data are heterogeneous (e.g. which would be expected if some sites or habitat types had a consistently stronger deviation from the proposed models; tests for heterogeneity: *Lognormal*: $Q_{df=63}$=24,8, p=1,0, *logseries*: $Q_{df=63}$=50,3, p=0,877). A graphic display of effect sizes by habitat disturbance categories (in three disturbance classes, see chapter 3.1; data not shown) indicated greater, but clearly

	logseries	lognormal	broken stick
fit	61	70	46
no fit (p<0,05)	4	1	28
%fit	**93,8 %**	**98,6 %**	**62,2 %**

Table 3.4 shows the number of sites with significant and non-significant χ^2-tests for the goodness of fit of species frequencies from Sphingid samples to standard species-abundance distributions. Missing sites to the total of 93 are caused by insufficient data for χ^2-tests.

non-significant deviations from both models in undisturbed habitats. Deviations from expected frequency distributions were in some cases caused by more ‘very rare’ species than expected (two deviations from *logseries*, one from *lognormal*), in others by less ‘very rare’ species than expected (two deviations from *logseries*). No unusual features of the sampling sites were recognised among the deviating samples.

P-values for distribution fit are not influenced by sample size for the *lognormal* or the *logseries* distribution (Spearman rank correlations: $R^2<0,01$, $p>0,5$), suggesting that lack of statistical power is not the main reason for overall low rejection rates of the two tested models.

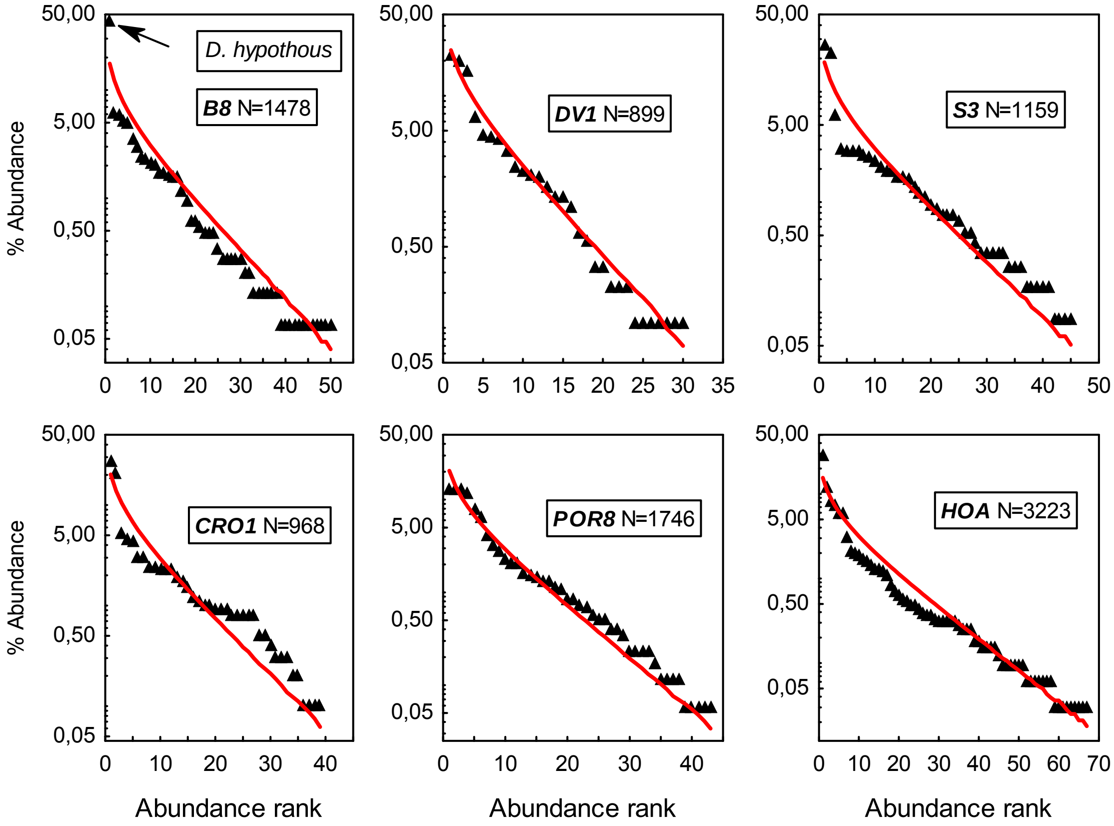


Figure 3.11 shows rank-abundance plots for the six largest local samples from Southeast-Asia (log-scaled y-axis). Red lines indicate expected frequencies from the *logarithmic series*. None of the sites does significantly (p<0,05) deviate from this distribution, but all except B8 and DV1 are better predicted by the *lognormal* distribution. See appendix I for site acronyms.

Local and regional rank-abundance relations

Hubbell (2001, p145) described the rank-abundance relations of local assemblages and ‘metacommunities’ (regional assemblage) in the framework of his neutral theory. Both are supposed to follow the *zero sum multinomial* distribution (*zsm*), which is similar to the *lognormal* for local assemblages, while it equals the *logseries* for an indefinitely large ‘metacommunity’ (Hubbell 2001). As a consequence of dispersal limitation, which leads to geographic autocorrelation of species’ population densities, rare species in the ‘metacommunity’ are even rarer in local samples, resulting in a ‘tailing off’ of rare species if rank-abundance plots of local and regional assemblages are compared. Following Hubbell’s

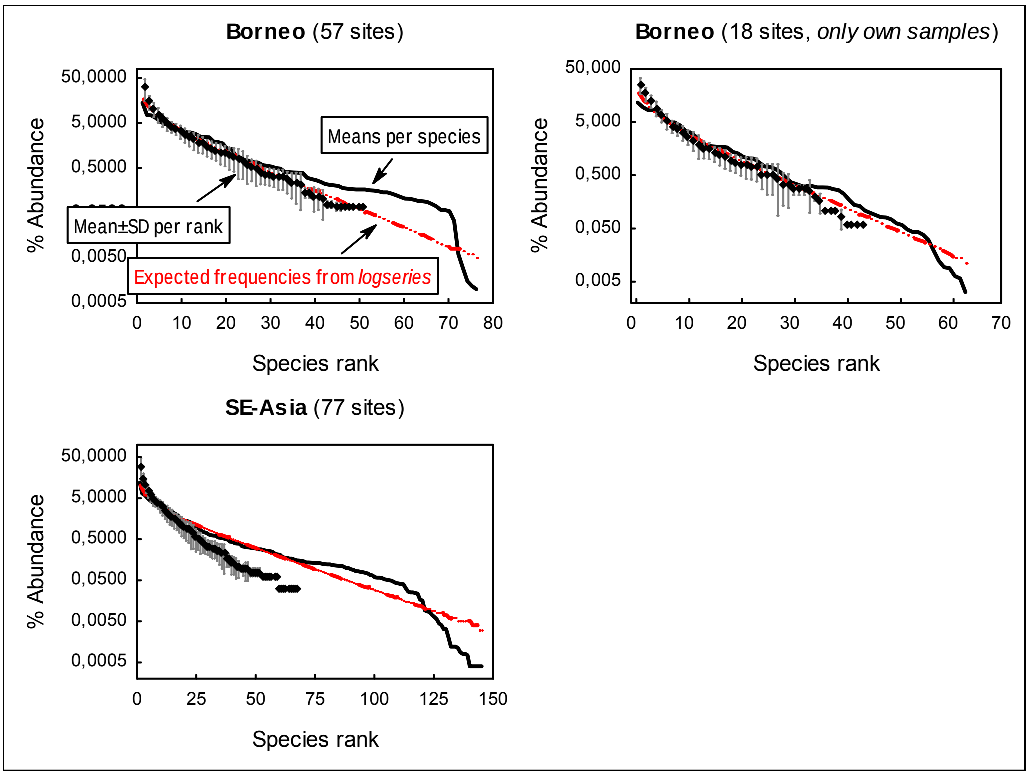


Figure 3.12 shows species frequencies for regional assemblages (solid lines, species means from local samples) and means±SD for ranks in local samples (see text for further details). Data from Seram & Sulawesi were not included in Southeast-Asia samples, hence the reduction in sample sites.

(2001) display of an example of neotropical tree data, 'metacommunities' of regional Sphingid assemblages (means for species across local samples, not transformed) and mean frequencies in local samples (means for ranks) are displayed in figure 3.12. The *logseries* distribution was fitted to data from regional assemblages. Despite several shortcomings in this approach (see discussion), the similarity to Hubbell's (2001) graphs is obvious. Local samples are 'tailing off', i.e. rare species are rarer than in the regional assemblage. However, regional data do also not fit the idealised *logseries* distribution, but have rarer-than-expected species. If only data from own sampling in Borneo are plotted, differences between the curves blur as even pooled samples do not sufficiently display the 'metacommunity'. If, on the other side, data from sites across SE-Asia are plotted, the difference between local and regional assemblages is more obvious. This must be expected, as biogeographic effects (i.e. the absence of certain species from some sampling regions, chapter 4.1) enforce Hubbell's (2001) hypothetical dispersal limitation, which diminishes rare species' frequency in local samples. Fitted *logseries* frequencies are lower (on the y-axis) than in Hubbell's (2001) graphs, which display the *zms* distribution. This is probably a consequence of the fitting procedure, as Hubbell (2001, chapter 9) states that the *zsm* is best fitted to the left half (the more abundant species ranks) of data. Such fitting to parts of the data could not be done with the *logseries* distribution, which is used as a supplement for the *zsm* here.

Phylogenetic independence of species frequencies

The *Test for Serial Independence* (Reefe & Abouheif 2003) yields a mean observed *C-statistic* that is significantly larger than that from randomized data; in only 105 of 3000 randomizations it is equal or larger than the observed mean of 0,111. This indicates that the null-hypothesis of phylogenetic independence is rejected at p=0,035: Mean species frequencies are influenced by phylogeny.

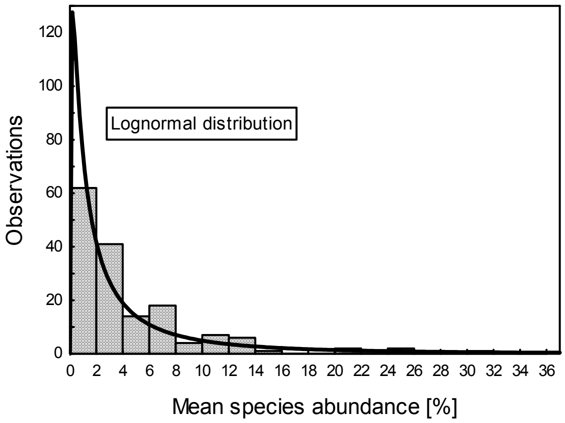


Figure 3.14 shows observed mean frequencies for species (over all sites) and an expected *lognormal* distribution. Data do not fit the *lognormal* (see text), but not because of a skew towards more rare species, as was frequently observed (Nee et al. 1991, Hubbell 2001).

Mean frequencies of species from taxonomic sub-groups were tested for differences. No significant differences were found between subfamilies (KW-Anova: N=159, $H_{df=2}$=0,910, p=0,635), nor between tribes (KW-Anova: N=159, $H_{df=5}$=6,201, p=0,287), but (barely) significant differences can be found on the level of genera (KW-Anova: N=159, $H_{df=44}$=61,067, p=0,045). Despite a weak p-value, this non-parametric test confirms systematic differences in phylogenetically different groups.

Discussion

Explanatory models of the species-abundance relation

The *lognormal* distribution was found to be the best standard model (Southwood & Henderson 2000) to describe the species-abundance relations of Sphingid moths from light trapping samples across Southeast-Asia. The almost ubiquitous fit of this model to species-abundance relations (see references above) is derived from the *Central Limit Theorem* of statistical sampling under the assumption of geometric population growth of species (May 1975, Southwood & Henderson 2000). Thus, despite attempts of providing a biological justification for the overwhelming empirical support of this model (e.g. May 1975), log-normality may be a general property of large heterogeneous natural samples where many unknown processes interact (McGill 2003b). Holloway (1996b) found that ecologically different subsets of a *lognormal* distributed moth fauna were also *lognormal* distributed. Furthermore, even 'non-biological' data such as wealth in the US, or human population among the worlds nations, are *lognormally* distributed (May 1975). McGill (2003a) criticized the *zms* as non-parsimonious when compared to *lognormal* – although the former is derived from basic principles of population growth, whereas the latter is an empirically well-proven model that, however, is based on multiple, unknown statistical sampling processes. While this matter cannot be treated here in more depth, a broader discussion of 'parsimony' in this context would probably benefit the analysis of species-abundance models, as it will get more and more difficult to objectively compare the goodness-of-fit of increasingly better fitting models (see also Bell 2003, Alsonso & McKane 2004). Comparisons of curve fit are considered a weak test of the underlying macroecological theories because a) several proposed mechanisms can yield the same curve, b) free parameters can fit almost any function to data, and c) different measures of fit to data yield different judgements of what functions ‘fits’ the data best (McGill 2003b). Stronger tests of macroecological theories would involve more precise, and multiple, predictions of curve parameters under different situations (ecological or scale-related; McGill 2003b).

Methodological constraints on measures of relative abundance

Data on species abundance in samples stem from light-trapping, which has two potential weaknesses: Light-trapping abundances are strongly influenced by not habitat-specific effects of weather, moonlight and surrounding vegetation (e.g. Yela & Holyoak 1997), and species might be unequally attracted to light (e.g. Kempton & Taylor 1974). The latter methodological problem has been thoroughly discussed in chapter 2. While the effect is certainly present in some species, it probably does not create a large bias in light-trapping samples. Species-abundance relationships have been successfully analysed in light catches of Lepidoptera, and no general biases were observed when compared to data from ‘unbiased’ samples such as vegetation counts (e.g. May 1975). The influence of parameters like weather and moonlight (which cannot be standardized under realistic field sampling conditions), on the other hand, lets absolute abundance of species at the light become almost worthless – only a conversion to relative abundance within a catch (frequencies) creates figures that are comparable across sites. Treating frequencies as measure of local population size or density makes the assumption of equal productivity on the sites (with regard to the hawkmoth community). This is not a completely unreasonable approximation within a relatively homogenous region like insular Southeast-Asia, which has no huge gradients of light or water availability that would lead to great differences in primary production (see e.g. maps in Cramer et al. 1999). However, some differences in productivity do certainly exist, which diminishes the exactness of data if frequencies are viewed as an approximation of population density.

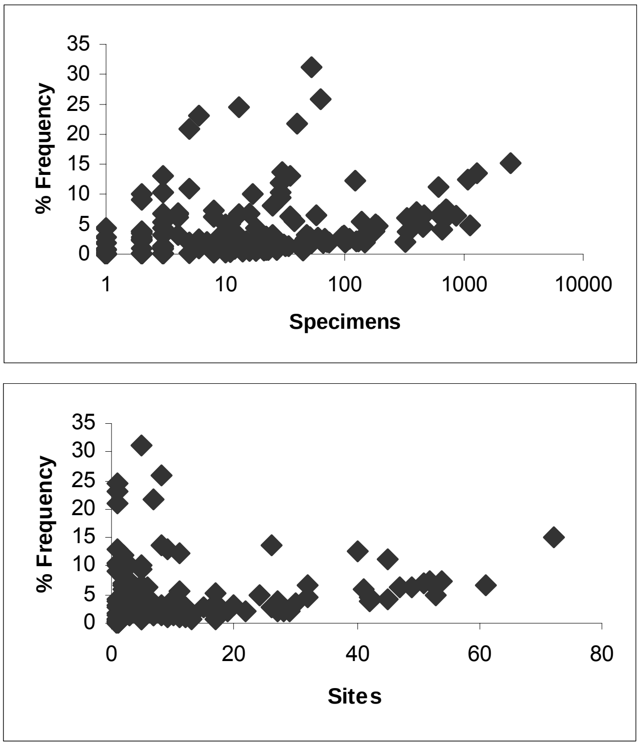


Figure 3.13 shows the relation between absolute abundance of species in pooled samples and their mean frequency (upper graph, abundance on $\log_{10}$-scale) and the number of occupied sites and species' frequency (lower graph).

Sample sites are neither from a homogenous habitat (which would be assumed by neutral models on species-abundance relationships, e.g. Hubbell 2001), nor are there large numbers of randomly chosen sites which would reflect the available habitats in a region in correct proportions. Rather, logistics are probably the most important factor on sample site choice. In Borneo, data from all major habitat types are available (although some did not find their way into analysis due to low specimen counts, e.g. mangrove or heath forest), whereas samples from the rest of Southeast-Asia might be non-representative chance samples. As a consequence, average frequencies derived from this data might be poor in representing mean population density across the continent even without the potential biases discussed in the paragraph above.

Figure 3.13 exemplifies the combined effects of these potential flaws in data quality: In a perfect world, where all samples are from the same habitat type, and there are no differences in local productivity or trapping efficiency, absolute sample size of a species, the number of samples where a species is present, and a species' frequency were perfectly correlated. This is obviously not the case, although correlations are significant (Spearman rank correlations, $R>0,352$, $p<0,001$). Species frequencies vary considerably over their range, probably at least partly as a result of varying local habitat conditions. No obvious geographic patterns (e.g. a decline in local frequency near the limit of a species range) could be observed in the most common species, for which such mapping was possible (data not shown).

The biases could be expected to blur whatever pattern could be found in the distribution of mean population densities. On the other hand, good models of species-abundance relations on a geographically large scale have to consider, or be at least robust to, habitat heterogeneity. It will still take a long time until flawless data for tropical invertebrates become available on a sub-continental geographical scale, so for the moment whatever data are there should be used to explore patterns and hypotheses – albeit with caution and an open eye for potential biases (Lawton 2000).

Patterns of species frequencies distributions and the neutral model

Despite the limitations due to data quality which are discussed above, patterns of mean frequencies in regional and local assemblages strongly resemble those predicted by Hubbell's (2001) theory of non-specific population growth of species (i.e. ecological neutrality; for discussion of the theory, see also Ricklefs 2003, Hubbell 2003). Furthermore, deviations from predictions (e.g. the 'tailing-off' of rare species even among the 'metacommunity' samples) or differences between subsets of data (e.g. Southeast-Asia *vs.* Borneo) can be readily explained and interpreted by the proposed effect of dispersal limited populations. Thus, on the not-so-rigorous level of graphic resemblance (e.g. McGill 2003a, b) Sphingid data support Hubbell's (2001) suggestions on a far larger geographical scale than the examples presented in his book. However, correct prediction of observed patterns does not necessarily prove the correctness of underlying assumptions, i.e. the ecological neutrality of species in Hubbell's (2001) theory (e.g. Purves & Pacala, in press). Sphingid assemblages are clearly influenced by habitat conditions (disturbance, elevation; see chapter 3.1), which indicates that species have differential success in different habitat types (i.e., 'niches'). On the other hand, predicted patterns persisted even though very heterogeneous data from various habitat types were used. Hubbell (2001) concludes that possibly the specialization of species does not have much impact on many community-level patterns of the system – an interpretation that is supported by Wilson & Lundberg (2004) who showed in simulations of multi-species communities that species-abundance relations are not influenced by interspecific interactions (as long as they are weaker than intra-specific ones).

Following the Central Limit Theorem, pooling of data from heterogeneous habitats (thus, data of heterogeneous assemblages) would result in a *lognormal* distribution (see also Holloway 1996b), which is rejected for pooled Sphingid data in a χ^2-test of mean frequencies (frequencies in octaves, $\chi^2_{df=9}=22{,}07$, $p<0{,}001$; see figure 3.14). Possibly the use of means from the relative abundance of each species over a number of sites is creating errors here, as data are not normally distributed - but transformation is not an option here as it would explicitly destroy the pattern that is searched for. It may be interesting in this context that Ulrich & Ollik (2004) also did not find a good fit to distribution models for data on mean densities of Hymenoptera in a German forest. A method is available to fit the *zsm* to data (instead of the surrogate *logseries* that was used in figure 3.12) and test it for significant deviations (McGill 2003a, computer program as 'C' source code), but it was found unpractical to use the computationally demanding process here.

Is the frequency of species in an assemblage ruled by phylogeny?

Life history traits of extremely rare and extinction-prone species can be predicted to a certain extent, despite a handful of contrary examples (e.g. Kunin & Gaston 1997). Among the main 'proximate' reasons for extinction are local rarity and restrictions in range size (Kunin & Gaston 1997, Keith et al. 2000, Alpizar-Jara et al. 2004, Gotelli & Taylor 1999), which are often correlated within a taxonomic group (e.g. Brown 1984, Maurer 1999, chapter 6). A number of species' characteristics have been proposed to influence both (e.g. niche breath, vitality rates; Gaston et al. 1997), thus creating the correlation of local abundance and range size. While observed patterns of variation in frequency or range size (see also chapter 4) both could be found among practically 'neutral' species (e.g. Bell 2000, Hubbell 2001), there are a large number of heritable traits that could cause one or the other.

A significant (though not particularly strong) phylogenetic autocorrelation was found in the data of mean frequencies of species: Related groups of species share features which lead to similarities in mean frequency within these groups. This finding has two implications: (1) Not surprisingly, hawkmoths in SE-Asia are not correctly described as assemblages of ecologically neutral species (e.g. Hubbell 2001), even if frequency distributions match patterns that would be expected in such an assemblage (see also Bell 2003, who reviews the problem of differentiating between empirical, adaptionist patterns and those predicted by neutral models). Not only do species exhibit different frequencies under different environmental conditions (chapter 3.1), which shows some degree of habitat preference, but (2) there are general features in taxonomic units which determine to a certain extent if a species is frequent or not. This fits with the notion that usually a species' relative abundance is retained over a relatively long time and might be an inherent property of a species (McGill & Collins 2003, Hadly & Maurer 2001; see also Sutherland 2004 and references therein for traits of 'weediness'). For the Sphingidae in Southeast-Asia, adult life expectancy or other parameters that are connected to different strategies of resource use between subfamilies (e.g.

Lemaire & Minet 1998, see chapter 1.2) could be suspected, but no significant differences in mean frequency were found between subfamilies or tribes (see above). Body size, which has been associated with abundance (e.g. Ritchie & Olff 1999) and species diversity (e.g. Godfray & Lawton 2001), is apparently not an explanatory factor for local frequencies: Body size measures are normally distributed in local samples (chapter 5.2) and do not correlate with mean frequency (chapter 6). Potentially influential features could be the degree of polyphagy of caterpillars, which correlates with mean species frequency (but not if controlled for phylogeny: chapter 6) or any other so far unidentified life history variable which makes some taxa more 'vital' (Holt et al. 1997) than others.

CHAPTER 4 - REGIONAL FAUNAS

CHAPTER 4.1 - SPECIES RICHNESS AND BIOGEOGRAPHY

Abstract

Major patterns of the species richness and biogeography of the Sphingidae in the Malesian archipelago were investigated. Using a compilation of specimen-label databases, a GIS-supported method was used to assess species ranges from records, which allowed combining habitat modelling approaches with the flexibility of considering additional information on species and sites (were available). Range maps for all species and checklists for 114 islands can be found at *http://www.sphingidae-sea.biozentrum.uni-wuerzburg.de*.

The estimated species richness of islands in the region is determined by islands size and biogeographical association. Species-area relationships are not close to linearity (on a double logarithmic scale) for the whole, heterogeneous region, and are so only for some of the more homogenous sub-regions.

Species proportions of Sphingidae subfamilies change with the geographic position of islands, while island area and the presence of large rainforest blocks appear to be non-significant parameters in a multivariate analysis. Furthermore, faunal turnover of islands in relation to distance between islands is steeper for Smerinthinae than for other subfamilies. These differences are discussed in the light of life history differences between the subfamilies.

Phenetic analyses of island fauna similarities reveal 'textbook'-like patterns of biogeographical associations in the region, with Wallace's line emerging as main faunal discontinuity in the region. Further analyses, using 'nestedness temperature calculation' and partial Mantel statistics, indicate that historical features of geography (such as geology and landbridges due to lower sea levels) are an important determinant of faunal similarity, but recent dispersal could also explain a significant portion of today's hawkmoth distribution.

Introduction

The Malesian archipelago has been an area of intense biogeographical analysis since A.R. Wallace (1869) realised the influence of geological history on the distribution of animal and plant species (for recent examples, see e.g. Holloway 2003, Hall & Holloway 1998). Lowered water levels during long periods of the Pleistocene (see Voris 2000), climate changes (e.g. Morley & Flenley 1987) and tectonic movements (Hall 1998) were suggested to be responsible for the observed large-scaled faunal and floral discontinuities such as Wallace's, Weber's and Lydekker's line (see e.g. maps in Monk et al. 1997) as well as finer-grained patterns within islands (e.g. vertebrates in Sulawesi: Musser 1987, termites in Borneo: Gathorne-Hardy et al. 2002b). An overview over established patterns, including a thorough treatment of the Lepidoptera in the region, can be found in Withmore (1981, 1987) and Hall & Holloway (1998). However, dispersal, extinction and speciation (which are dependent on isolation and size of islands rather than their history) add stochasticity to data and blur the 'geological signal' in species distribution, thus challenging both the understanding of patterns as well as the application of suitable analysis methods (Holloway 1998b, 2003).

Modern biogeographical analysis investigates regional relationships based on the phylogenetic relatedness between taxa (see e.g. Avise 2000), leading to information that is often neglected in community ecology and biodiversity research (Wiens & Donoghue 2004). Cladistic methods (e.g. component analysis, parsimony analysis: Kitching et al. 1998) produce pedigrees of regions that describe the evolutionary history of biotas. However, a number of factors make such a cladistic q-mode approach difficult in the Southeast-Asian region even if the phylogeny of monophyletic groups under investigation was known. Due to the geological complexity of the region it is difficult to represent hypotheses of the geological evolution in a dichotomous tree structure (Holloway 1998b, 1982, Metcalfe 1998). Furthermore, a high degree of sympatry, caused by many widespread species (see also chapter 4.2), leads to a large number of possible cladograms of regional relationships (Holloway 1998b).

Less rigorous, but not necessarily less precise than cladistic methods under conditions of insufficient data (Holloway 1998b), are phenetic q-mode analyses, whereby regions are ordinated according to similarities of their fauna. These methods are commonly employed in community ecology (e.g. Southwood & Henderson 2000) and do not require knowledge of the phylogeny of involved taxa. Phenetic methods are a precursor to cladistic analytical methods (see e.g. Baker et al. 1998) and are still successfully applied to investigate geological hypotheses (e.g. de Jong 1998, see also Kitching et al. 2004). Furthermore, recently refined statistical methods for testing the effect of vicariance on species ranges against adequate null models (e.g. Hausdorf & Henning 2003) might bring further value to these approaches.

Holloway (1987b) has identified faunal regions for Malesian Lepidoptera which reflect aspects of the geological history of the region, but also show a strong component of modern-day geography that indicates the importance of dispersal processes (Holloway 1998b). Based on a phenetic analysis of butterflies and some moth taxa, 'Wallacea' (comprising the Philippines except Palawan and Sulawesi) was identified as a transitional region between Sundaland in the west and Melanesia (comprising the Moluccas, New Guinea, the Bismarck Archipelago and the Solomon Islands) in the east, while the Lesser Sunda Islands were loosely associated with Sundaland. Sulawesi houses a fauna that was mostly shaped by dispersal rather than by vicariance of a larger land unit (Holloway 1997b) and appears as a pivotal point for the understanding of Lepidoptera patterns in the region. Endemism on Sulawesi is high and biogeographic relations can be found with the Philippines, the Moluccas, and the Lesser Sundas, depending on the taxon and the habitat (i.e., altitudinal zone) under investigation (Holloway 1997b), yet similarity to nearby Borneo is relatively low (Holloway 1998b).

The species richness of many organisms is known to change along environmental gradients - altitude (e.g. McCoy 1990, Wolda 1987, Bachman et al. 2004, Gentry 1988, Holloway 1987c), disturbance (e.g. Beck et al. 2002, Lawton et al. 1998, Schulze et al. in press) and productivity (e.g. Bonn et al. 2004, Gaston & Evans 2004, Rajaniemi 2003, Cornwell & Grubb 2003; the latter two are often interacting, e.g. Connell 1978, Huston 1994), are often important at a local scale, whereas area size (Hoyle 2004, Ulrich & Buszko 2003, Rosenzweig 1995, Connor & McCoy 1979, Preston 1962a, b) and latitude (Willig et al. 2003, Chown & Gaston 2000, Johnson 1998a, Rosenzweig 1995, Pianka 1966, Currie et al. 2004, see also Reid 1998, Leigh et al. 2004) become increasingly important at larger geographic scales. Furthermore, isolation and size of islands influence immigration, extinction and speciation rates, and thus species richness (Whittaker 1998, Rosenzweig 1995). Additional to such direct or indirect ecological effects, historical changes of geography disrupt the equilibrium of communities and can lead to differences in species richness between ecologically very similar regions (e.g. Holloway 1987b for Lepidoptera in the Indo-Australian region, Gentry 1988 for tropical trees, Diamond 1972 for birds, see also Whittaker 2000, Hengeveld 1990, Ricklefs 2004). Dispersal ability is probably a key feature for such differences (see e.g. Holloway 1996) as it influences the duration that patterns caused by historical distribution limits can persist (e.g. Lomolino 2000). Consequently, different patterns of species richness on island groups can be found between taxa with differing dispersal abilities (e.g. Diamond 1972, 1973, 1975, Diamond & Mayr 1976, Holloway 1998b, for further examples see Begon et al. 1996).

In the present analysis it shall be explored,

(1) if Sphingidae show similar patterns of faunal similarity as they were previously established for other Lepidoptera (as described by Holloway 1987b, 2003, see above), and

(2) to what degree observed patterns can be explained by known patterns of geological and geographical history.

Furthermore, it will be investigated

(3) what geographical features influence the species richness of Sphingidae in the region, and

(4) what can be learned from the respective patterns of species richness and faunal similarity of taxonomic sub-groups of the Sphingidae.

Rarely employed techniques such as 'nestedness temperature calculation' of fragmented archipelagos (Atmar & Patterson 1993) and r-mode analysis (Holloway 1998b) are used to explore further information on biogeographical patterns and processes of the region.

Methods

1) Compilation of records

From published literature, unpublished species lists, museums and private collections more than 34.500 records for the worldwide distribution of all 375 species (and five undescribed morphospecies) of hawkmoths from 'Southeast-Asia' (from Burma/Myanmar to the Solomon Islands; see chapter 1.2, Beck & Kitching 2004 for details) were compiled. A complete literature listing, details on unpublished data sources (which, among others, cover the collections of the Natural History Museum in London, the Carnegie Museum in Pittsburgh, several online resources (e.g. Pittaway & Kitching 2003) and own sampling in the region) as well as additional information on data sources and their interpretation can be found in Beck & Kitching (2004). Much effort was undertaken to minimise errors (see Graham et al. 2004) by checking data for taxonomic inconsistencies (mostly following Kitching & Cadiou 2000 and recently published taxonomic literature) and by identifying the correct location of sampling sites. While ca. six percent of the records had original information on latitude and longitude of the sampling sites (usually recent records with GPS-data), the geographic position for most records had to be found with the help of internet resources and various modern and antique atlases. In a tedious procedure, latitude & longitude could be assigned with an accuracy of at least 1 degree (which creates a maximum error of ca. 160 km) to ca. 90 percent of the records. Ca. four percent of the records were not detailed enough to identify them on a 1°-grid (site information such as 'Southeast China' or 'Japan') and were tentatively assigned to the most likely region, based on collection year, infrastructure and the 'popularity' of regions for collectors. A small number of records (ca. 0,1 %) raised considerable doubt on their credibility for various reasons. Based on the likelihood of misidentifications in some species or the risk of mislabelling or misspelling in large collections, they were ignored for the estimate of species' ranges – however, future sampling might actually prove them right. Likewise, a number of records were considered credible yet were excluded from the range because they were believed to be stray individuals or vagrants far off their normal breeding range. In many cases this information came from the original data source, in other cases it was concluded from the rest of the records (e.g. species with a tropical distribution and a single specimen-record from South Australia or northern China).

2) Estimating range areas

The records were entered into a Geographic Information System (GIS, *ArcView 3.2*, 2000) where it was possible to display them by species, subspecies, record accuracy, altitude or year of sampling (if known). As a base map the world map of *ArcView* seemed sufficiently detailed, although some small islands in the Philippine and Moluccan region and the South Pacific were missing (these were hand-digitized from various naval maps and inserted into the world map where necessary). A number of GIS-compatible habitat maps can be downloaded from the internet (e.g. *http://www.geographynetwork.com, http://www.gvm.sai.jrc.it/glc2000*) and were used to 'underlay' the species records in order to find patterns of distribution. Altitudinal relief, vegetation zones, precipitation and minimum winter temperature often matched the outer limit of records, and a number of apparently important parameters for

Sphingid distribution could be identified (see also Quinn et al. 1997a, 1998, Cowley et al. 2000 for parameters affecting British Lepidoptera distributions): Minimum temperatures often seem to determine the northern limit of a species, whereas temperate species are often found only in montane areas on the southern, tropical boundary of their range. Besides main vegetation zones, precipitation is a very important parameter for tropical Southeast-Asian species, which thus often show distribution patterns with a 'finger' along the wet Himalaya foothills and a disjunct area in the wet Western Ghats, while the dry central part of India is left out. Likewise, many Southeast-Asian species are found in the Northern and North-eastern, wet parts of Australia, but not in the dry interior.

The limits of many species within Malesia, however, seem to be more determined by recent or historical geography than by habitat alone, so species ranges were not extended beyond actual records in that region. Generally, if in doubt a conservative approach that would underestimate rather than overestimate species' ranges was preferred. Subspecies division often gave important clues if gaps in the records indicate genuinely disjunct ranges, or if they are just a result of undersampling. The uneven sampling effort in different regions is disturbing this so far straightforward procedure (see also Graham et al. 2004, Fagan & Kareiva 1997, Soberón et al. 2000) - a missing species in well-sampled northern Thailand or Northeast Borneo indicates its absence from that region, while it doesn't mean much in undersampled Laos, Burma/Myanmar, the Solomon Islands or Southern (Indonesian) Borneo. Furthermore, certain species (e.g. day-active *Macroglossum* or *Cephonodes*) are more likely to be overlooked or misidentified than others.

Considering all these factors, the best possible estimate of each species' range was digitised - which nevertheless might have to be corrected if further extending records are found. All range maps and island checklists as well as more details and an example of the process of range estimation can be viewed in Beck & Kitching (2004). Some very common and widespread species migrate during favourable seasons into regions where they cannot permanently persist (mostly tropical species into Europe, northern China, or temperate Australia; e.g. Gatter & Gatter 1990, Ohba et al. 1999). In these cases the range estimates were separated into permanent and migrant ranges, usually based on information from very well-surveyed regions such as Europe, South Korea or Japan.

Similar approaches to estimating Lepidoptera species ranges have previously been used in computerised (e.g. Cowley et al. 2000) and non-computerised (Hausmann 2000, pers. com.) form. The use of GIS not only makes it easier and more precise to find distribution patterns by overlaying the records with maps of potentially important habitat parameters, but it also allows to use the resulting range maps for further computer-aided analysis. Area sizes and other measures of distribution can easily be calculated from the range estimates (e.g. Hooge et al. 1999) and recorded as well as estimated species checklists for regions (countries, islands or grid-squares) can be extracted from overlaid range maps (see Beck & Kitching 2004). However, no explicit computer model was used here to estimate ranges (see also Holloway et al. 2003 for a 'semi-computerised' habitat model). Computer models have been successfully used for range estimates on a smaller geographic scale (e.g. Raxworthy et al. 2003, Ray et al. 2002, Iverson & Prasad 1998) and would be desirable for their fast applicability to a large number of species. Despite the apparent 'subjectivity' of the approach which was chosen here, a 'brain-model' (as opposed to a computer model) is probably still more precise due to an easier consideration of species differences, be it ecological requirements, if known, or recording constraints. The analysis of presence-only data that is typical for museum data (Graham et al. 2004) is still problematic for statistical habitat models (e.g. Zaniewski et al. 2002). Moreover, some models were found to under-estimate the habitat occupancy of highly mobile species (e.g. Cowley et al. 2000). However, the rapid methodological advances make computerised GIS models a very promising future option (e.g. Segurado & Araujo 2004, Engler et al. 2004, Rushton et al. 2004, Lehmann et al. 2003, Mackey & Lindenmayer 2001).

3) Analyses of faunal similarity

Checklists for islands of the Malesian archipelago (including the Malay Peninsula) were extracted from the range maps and used for phenetic analyses of biogeographical patterns, ignoring faunistic patterns that occur within some islands (e.g. West Java *vs.* Central and East Java, mountain regions *vs.* coastal lowlands on Sumatra or New Guinea). Only analyses of estimated data on island faunas, which yielded clear and readily interpretable results, are presented here. Recorded data, on the other hand, did not perform well, presumably due to the effects of undersampled faunas on all but the largest islands of the archipelago, although lower-order clustering often matched that of estimated data (see data in Beck & Kitching 2004).

As a first step of analysis, nested island faunas (faunas that are completely contained in some other, typically nearby and larger island) were identified and excluded from analysis, as they disturb the clustering and ordination processes (Holloway 2003). Of the 114 'islands' (113 & Peninsular Malaysia) for which data were available, 38 'genuine' island faunas remained for further analyses. Preston's (1962b) coefficient of faunal resemblance was used in combination

Map 4.1: Distribution of estimated species richness for Southeast-Asian Sphingidae.

with single-linkage cluster analysis, which was considered suitable for the analysis of archipelagos with island chains (Holloway 2003). Preston's coefficient is derived from principles of the species-area relationship (see Rosenzweig 1995 for a review) and has some interesting properties for biogeographic analysis: If z, which measures the relative faunal distance between two samples from zero to unity, is below the equilibrium value of 0,27, the samples can be considered to stem from the same region (i.e., there is faunal exchange). If, on the other hand, z >0,27, then "there is, and has long been, some degree of genuine isolation" (Preston 1962). Coefficients were calculated according to the table in Preston (1962). As the results of clustering and ordination techniques are often heavily dependent on the employed method (e.g. Holloway 2003, Southwood & Henderson 2000, Hengeveld 1990), several other approaches were used to confirm or discuss the resulting patterns. Nonmetric Multi-Dimensional Scaling (MDS, Legendre & Legendre 1998) of Sørensen-indices or cluster analyses based on Bray-Curtis coefficients (also termed 'percentage difference', this index is related to the Steinhaus distances and to Sørensen indices if only presence-absence data are used; Southwood & Henderson 2000, Henderson & Seaby 2002) can be found in Beck & Kitching (2004). There is generally great controversy on the calculation of similarity or β-diversity (Koleff et al. 2003), and no single measurement or index can perfectly consider all aspects of this concept. Cluster analyses and other ordination techniques were computed with the programs *Statistica 5.01* (StatSoft 2003) and *Community Analysis Package 2.04* (Henderson & Seaby 2002).

Results

1) Species richness, subfamily proportions and faunal turnover

The species richness of Sphingidae in Southeast Asia seems to be governed by two major gradients (see map 4.1): A general decline of species numbers from the oriental mainland in the Northwest to the insular regions in the Southeast, and an effect of area size, whereby larger islands house more species than smaller ones. Area size, for which an effect on species richness must be expected (e.g. Plotkin et al. 2000, Rosenzweig 1995, Connor & McCoy 1979, Preston 1962), co-varies with geographic position as well as major biogeographical boundaries. A multivariate model (General Linear Model, GLM: Guisan et al. 2002, Rushton et al. 2004, StatSoft 2003)

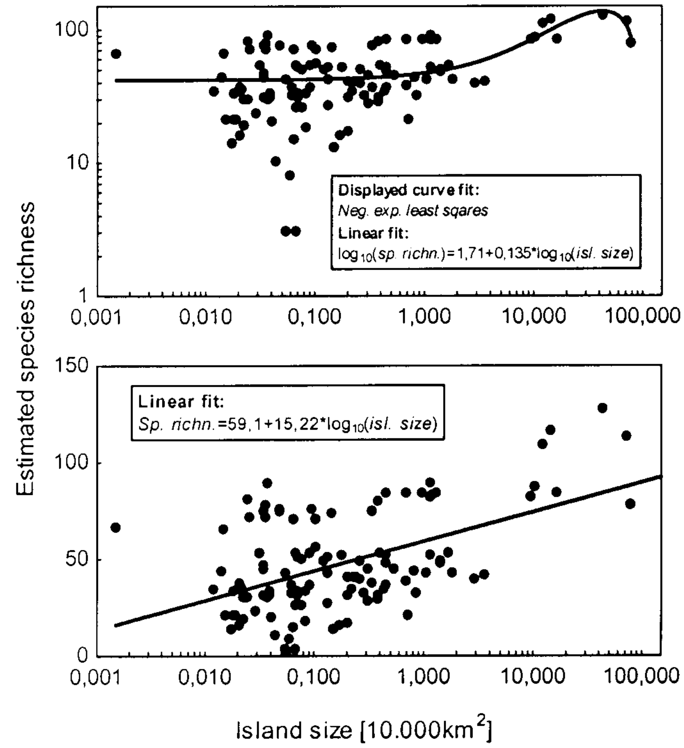


Figure 4.1a shows the species-area relationship for Sphingidae of the Malesian archipelago on a double-logarithmic plot ('power curve', upper graph) and a semi-logarithmic plot ('exponential curve', lower graph).

was used to test effects on the estimated species richness of 114 islands. Latitude, longitude and $\log_{10}$(island area) are continuous variables in the model, while main biogeographical regions (Andamanes, Sundaland, Lesser Sunda Islands, Wallacea, the Moluccas, New Guinea & surrounding islands, the Bismarck Islands and the Solomon Islands) were entered as categorical predictors. The model is significant at $R^2_{multiple}=0{,}675$, $F_{df=10}=21{,}389$, $p<0{,}0001$. Log_{10}(island area) ($F_{df=1}=64{,}126$, $p<0{,}0001$), latitude ($F_{df=1}=15{,}045$, $p<0{,}0002$) and region ($F_{df=7}=4{,}362$, $p<0{,}0003$) emerge as significant variables, while longitude ($F_{df=1}=0{,}026$, $p=0{,}871$) appears to play no independent role in the system. Latitude is positively correlated to species richness and probably reflects the proximity to the Southeast-Asian mainland rather than effects of climate or primary production. *Post hoc* tests (Fisher's LSD) reveal that independent of islands sizes both Sundaland and Wallacea are significantly richer in Sphingid species than other regions.

Figure 4.1a shows the effects of island area on species richness in the usual double logarithmic plot as well as on a semi-logarithmic plot (e.g. Scheiner 2003, Plotkin et al. 2000, Rosenzweig 1995, Connor & McCoy 1979, Šizling & Storch 2004). Species richness is significantly influenced by island area (see above), but the relationship is by far not perfectly linear on a double logarithmic scale, but curvilinear with a rather flat part in the lower range of island sizes. A 'small island effect' has been observed across a broad range of taxa and may be caused by habitat differences, stochastic disturbances, proximity to larger 'source islands' and biogeographic association (Lomolino & Weiser 2001 and references therein, Diamond 1972), although examples from the literature usually refer to considerably smaller figures of 'small' island size. A linear regression explains only a moderate proportion of the Sphingid data variance ($R^2=0{,}170$) and yields a slope of $z=0{,}135$, which is considerably lower

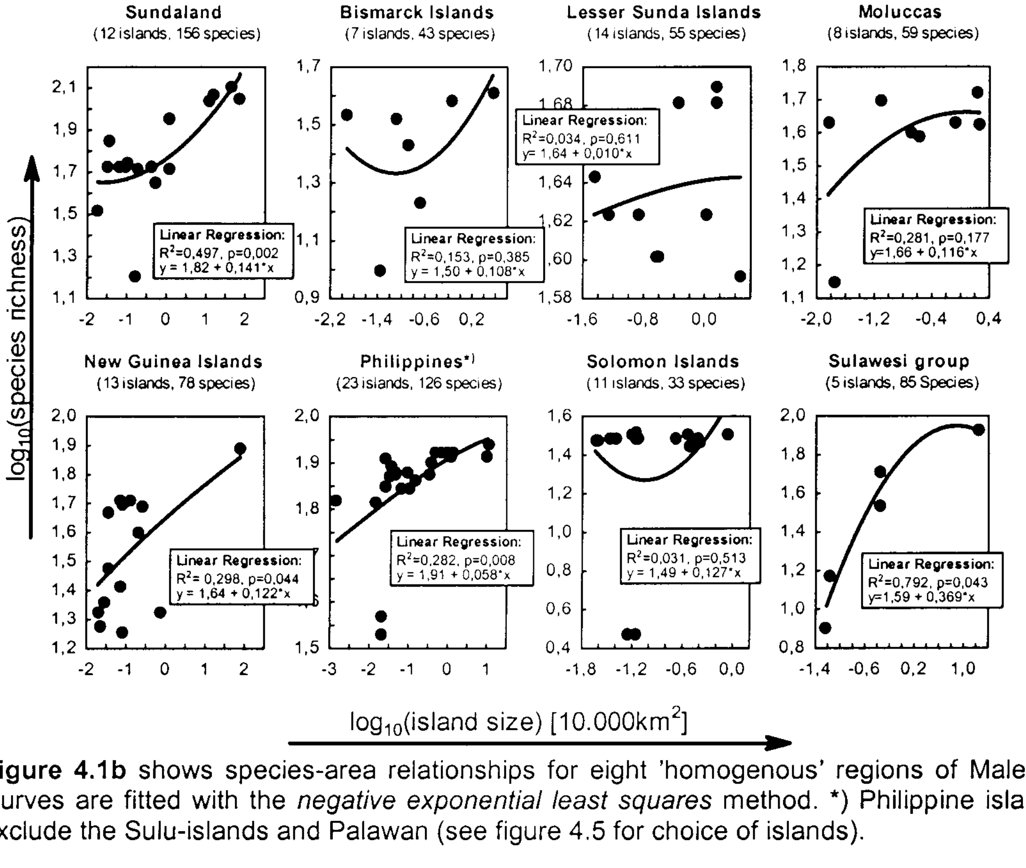


Figure 4.1b shows species-area relationships for eight 'homogenous' regions of Malesia. Curves are fitted with the *negative exponential least squares* method. *) Philippine islands exclude the Sulu-islands and Palawan (see figure 4.5 for choice of islands).

than what would be expected from the island biogeography theory of homogenous archipelagos (i.e., z=0,27, Preston 1962, see e.g. Rosenzweig 1995 for review). Data is much closer to linearity in a semi-logarithmic plot (figure 4.1a, lower graph), the relationship between island size and species richness follows an exponential function with R^2=0,263 (see Scheiner 2003 and references therein for a discussion of shapes of the species-area relationship). Recorded data (not shown) exhibit a similar shape of the relationship, but have a much steeper decline in species numbers on small islands. As a result of this, power-function fit to the data (i.e., linearity on a double-logarithmic plot) is better (R^2=0,413) and the slope of the regression is considerably steeper (z=0,449). Furthermore, data of recorded species show strong trends for more species at higher latitudes and at lower longitudes. However, the worst undersampling can be expected on small islands and in the remote Southeast of the archipelago, so all three observed effects are likely to be undersampling artefacts. Of eight species-area relationships within relatively homogenous regions (see below for classification) of Malesia only four are statistically significant (double-logarithmic plots, figure 4.1b), and most have similarly low z-values as the relationship for all islands. Only Sundaland and the Philippines show 'textbook'-like relations (Rosenzweig 1995). Species-area curves are expected to exhibit flatter slopes in non-predators than in predators (e.g. Hoyle 2004) and at geographic meso-scales (i.e. continent-wide), as opposed to local or world-wide scales (see Rosenzweig 1995, Lomolino & Weiser 2001, Allen & White 2003).

Large differences in sampling effort probably also bias estimates in mainland Southeast-Asia (map 4.1): The apparent decline in species richness in Burma/Myanmar, Cambodia and Vietnam might be an artefact of undersampling, while the declines in areas of strong anthropogenic habitat conversion (e.g. Bangkok area, North-eastern Thailand, or parts of the Thai peninsula) are possibly genuine. Regions with a mountainous relief often seem to hold more species than lowlands (e.g. within Sumatra, Borneo & New Guinea; data not shown, see range maps in Beck & Kitching 2004), which could have multiple causes: Sphingidae seem to have their peak of local species richness around 1000 meters a.s.l. (Schulze 2000, chapter 3.1), mountain regions generally have a higher γ-diversity due to their altitudinal zonation (e.g. Barthlott et al. 1996 for plants, Holloway 1976, Brehm 2002 for moths) and mountain ranges are not suitable for industrialised rice growing, which probably does not offer much suitable habitat for hawkmoths in parts of continental Southeast-Asia (I.J. Kitching pers. com.).

The relative species richness of the three subfamilies of the Sphingidae was compared along two gradients with potentially different effects on subfamilies, as concluded from life-history differences (chapter 1.2, Lemaire & Minet 1998) and patterns found in local habitat comparisons (chapter 3.1): (1) Smerinthinae were expected to thrive mainly in primary rainforest regions, while Macroglossinae may be adapted to disturbed habitats. Figure 4.2 shows comparisons of islands with and without larger blocks of rainforest for recorded and estimated island faunas. Data follow expected patterns of a lower frequency of Macroglossinae and a higher frequency of Smerinthinae on rainforested islands, but trends are not statistically significant. (2) Smerinthinae were expected to be inferior dispersers, therefore a decrease in their frequency was expected from the mainland towards the Eastern islands

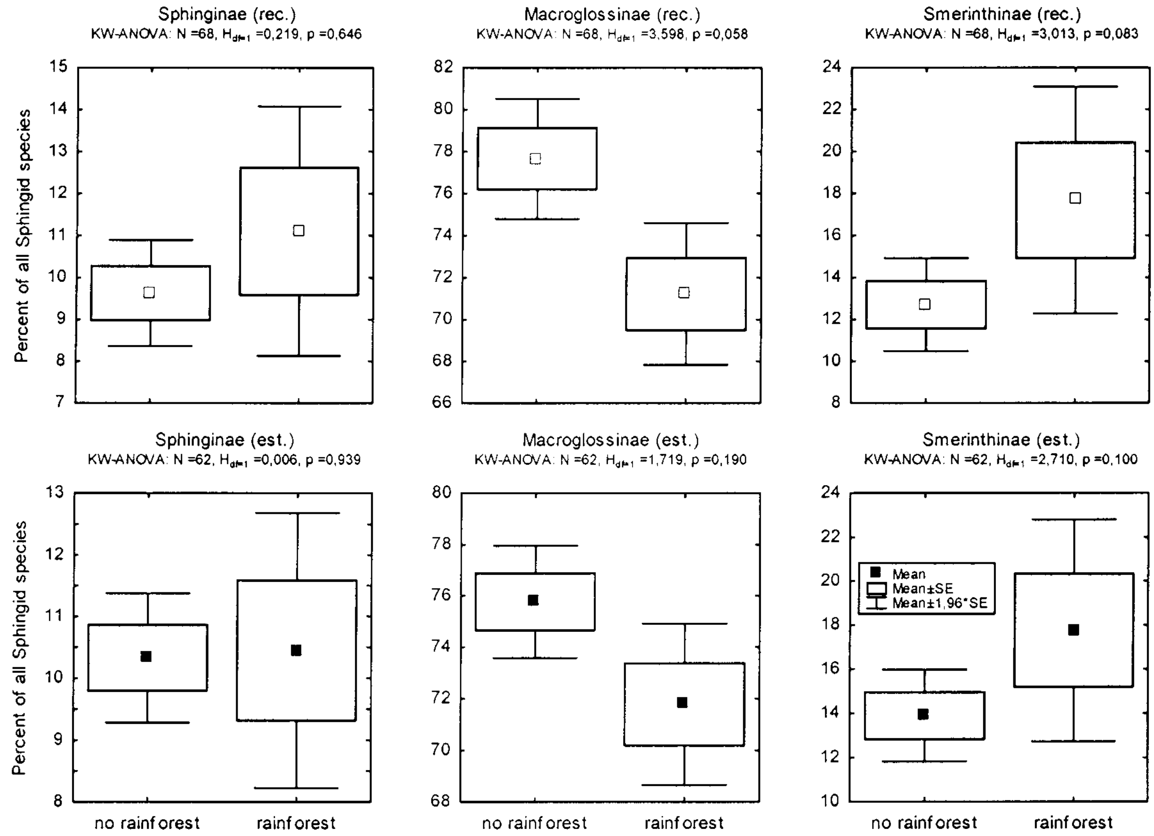


Figure 4.2 shows mean proportions of Sphingid families on islands with and without large rainforest blocks (classification mainly based on maps in Monk et al. 1997). The upper row of graphs is based on recorded data, the lower row on estimated island faunas.

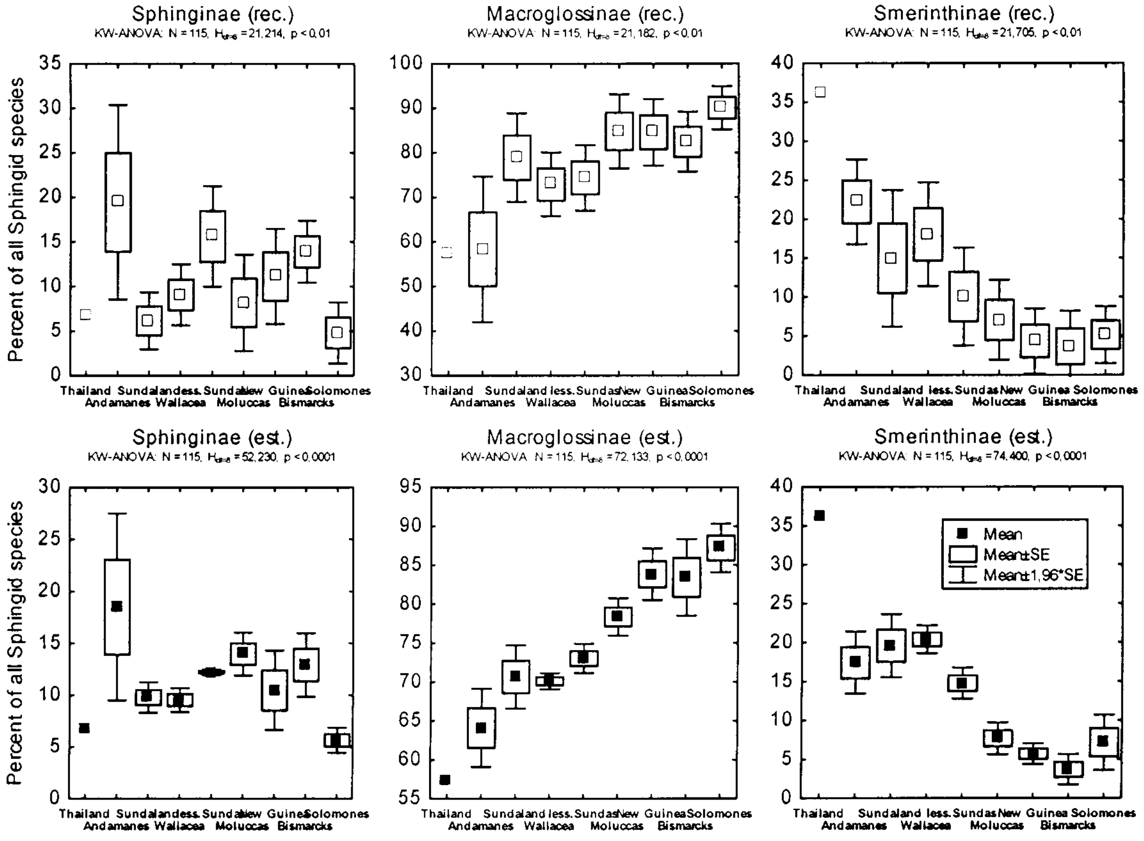


Figure 4.3 shows mean proportions of Sphingid subfamilies in different biogeographic regions of the Malesian archipelago. Additionally, data for Thailand are shown as an example of a continental Southeast-Asian fauna. Regions were arranged according to their longitudinal position. The upper row of graphs shows recorded data, the lower row estimated island faunas.

Variable	1-Wilks Λ	$F_{df=2}$	p
Log_{10}(island area)	0,001	239,18	0,973
Latitude	**0,255**	**0,03**	**<0,0001**
Longitude	**0,356**	**18,52**	**<0,0001**
Rainforest	0,028	29,91	0,220
Constant	0,816	1,54	<0,0001

Table 4.1 shows results of a multivariate GLM, testing various geographical variables for effects on the (estimated) proportions of Sphingid subfamilies in 114 island faunas. The model is significant for all three subfamilies:

Macroglossinae: $R^2=0,632$ $F_{df=4}=49,53$ $p<0,0001$
Smerinthinae: $R^2=0,495$ $F_{df=4}=28,67$ $p<0,0001$
Sphinginae: $R^2=0,062$ $F_{df=4}=2,87$ $p=0,026$

(figure 4.3). Univariate differences between the regions are significant and follow expected patterns (see also Holloway et al. 2001): The decline in the frequency of Smerinthinae from Western to Eastern regions is compensated by the Macroglossinae, while the Sphinginae follow a rather irregular pattern. However, island area, geographic position and rainforest blocks of Southeast-Asian islands are probably not independent: Islands tend to get smaller towards the Southeast, and rainforest areas appear more common on large islands (Monk et al. 1997). Effects on estimated proportions of subfamilies in island faunas were tested with a multivariate GLM, using 'rainforests' as categorical variable and latitude, longitude and log_{10}(island area) as continuous predictors. Results indicate that the proportions of Macroglossinae and Smerinthinae can be predicted to a high degree by geographic position alone (see table 4.1 for test details), while islands size and rainforest are insignificant co-variables. Preliminary trials with GLMs showed that longitude and biogeographic region had such high collinearity in this data set that they could not be tested within the same model. Longitude was therefore chosen as the more parsimonious variable (see also figure 4.3). Smerinthinae species gain in proportion with increasing latitude and decline with increasing longitude, while Macroglossinae show the reversed effect. On the Polynesian islands east of 168°E longitude no Smerinthinae are found, while some Southeast-Asian Macroglossinae can be found as far east as the Pitcairn Islands (longitude ca. 130°W). Sphinginae proportions are significantly (negatively) affected only by longitude, but show a much weaker relationship than the other subfamilies.

Changes of species proportions on the next lower taxonomic level of tribes indicate that (1) among the Sphinginae, the tribe Sphingini weakly follows a pattern of a lower proportion of species towards the East (in estimated data), while the Acherontiini do not exhibit any clear pattern. (2) Among the Macroglossinae, the Macroglossini (which are by far the dominant tribe in all communities) determine the pattern for the subfamily, while the Dilophontini are less consistent. The genus *Macroglossum* alone, unique because with 73 species it is the largest Sphingid genus in Southeast-Asia and has mostly day-active species, shows no consistent pattern. (3) Among the Smerinthinae, both larger tribes (Ambulycini and, very clearly, Smerinthini) follow the subfamily pattern of decline east of Wallacea. The small tribus Sphinglini does not occur east of Sundaland and Wallacea (and here only with three species).

Figure 4.4 shows faunal similarity as a function of distance between islands (but ignoring all other biogeographic effects). Non-parametric, Mantel-type permutation tests were used to establish the significance of the relationship between geographical distance of islands and β-diversity (measured by Sørensen indices) of the family Sphingidae as a whole, as well as the

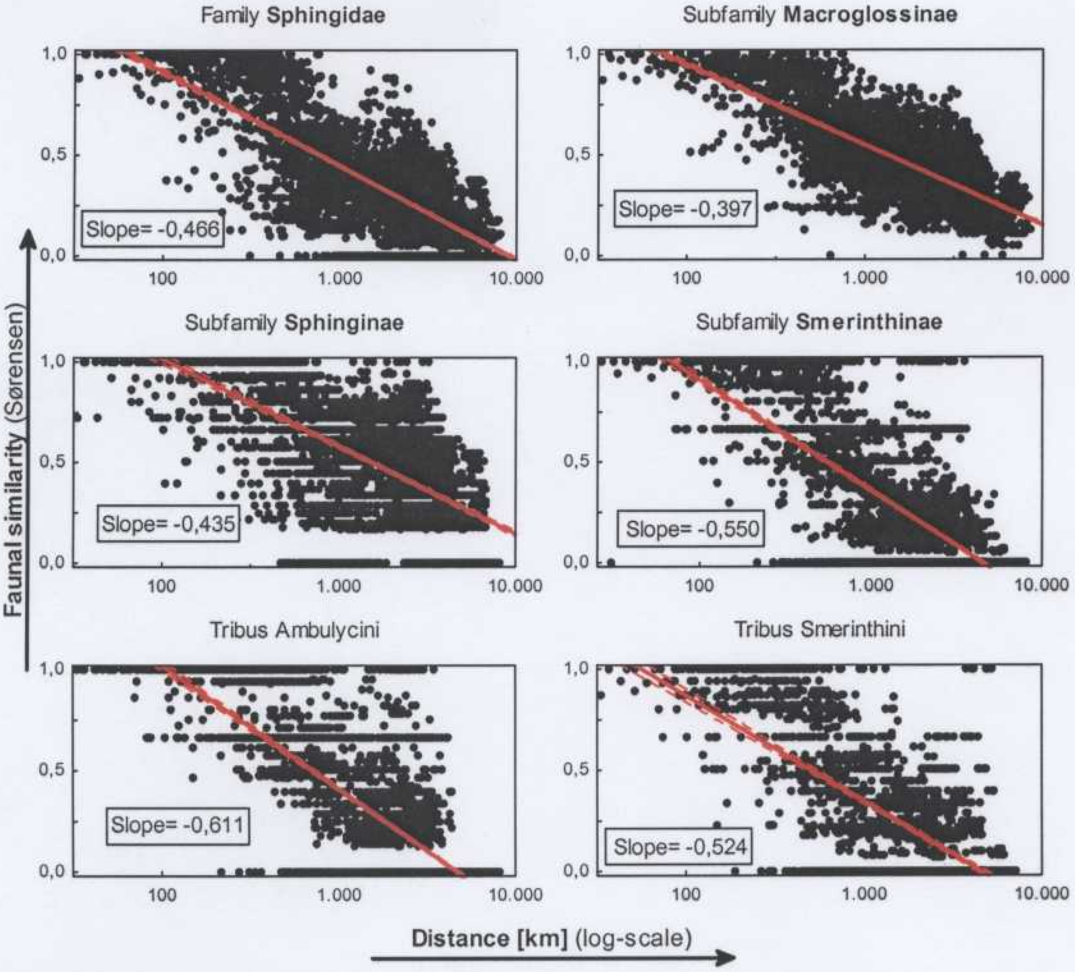


Figure 4.4 shows faunal similarity based on Sørensen indices of estimated island faunas in relation to distance between islands for all Sphingidae (upper left graph) and the three subfamilies separately. Statistical tests, including the 99% confidence intervals of regression lines, do not strictly apply as sample sizes are inflated with non-independent data in this representation, but a comparison of the regression slopes is still meaningful for Sphingidae as whole as well as the three subfamilies as the data refers (almost) to the same islands, therefore the sample size inflation is equal in all four graphs. Significance of the relationships is confirmed by a non-parametric randomisation test (RELATE, using the computer program *PRIMER 5* (2002), 10.000 randomisations). This method produces Mantel-type test results without any assumption about data distributions or linearity of the relation:

	Rho (Spearman's R, corrected for tied ranks)	N (occupied islands)	p
All Sphingidae	0,688	114	<0,0001
Macroglossinae	0,704	114	<0,0001
Sphinginae	0,601	111	<0,0001
Smerinthinae	0,665	108	<0,0001
Ambulycini	0,708	102	<0,0001
Smerinthini	0,466	80	<0,0001

three subfamilies and the two larger tribes of the subfamily Smerinthinae (see caption of figure 4.4. for test details). Distance emerges as a key predictor of faunal similarity (see also discussion), and there are clear differences in the slope of the relationship: Smerinthinae faunal similarities are considerably stronger (negatively) influenced by distance than the faunas of Macroglossinae or Sphinginae, indicating an inferior dispersal ability in the former group. The slope of the relationship between the two major tribes within the Smerinthinae, however, does not differ in an expected pattern: Ambulycini, which possibly share a similar life history with the subfamilies Macroglossinae and Sphinginae (see discussion and chapter 1.2) do not show a flatter, but a steeper slope than *capital breeding* Smerinthini. The latter group shows a considerably weaker distance-turnover relationship (lower R-value), which might indicate that other factors than present day geographic distance (e.g. ancient coastlines) were more influential in shaping the distribution of this group.

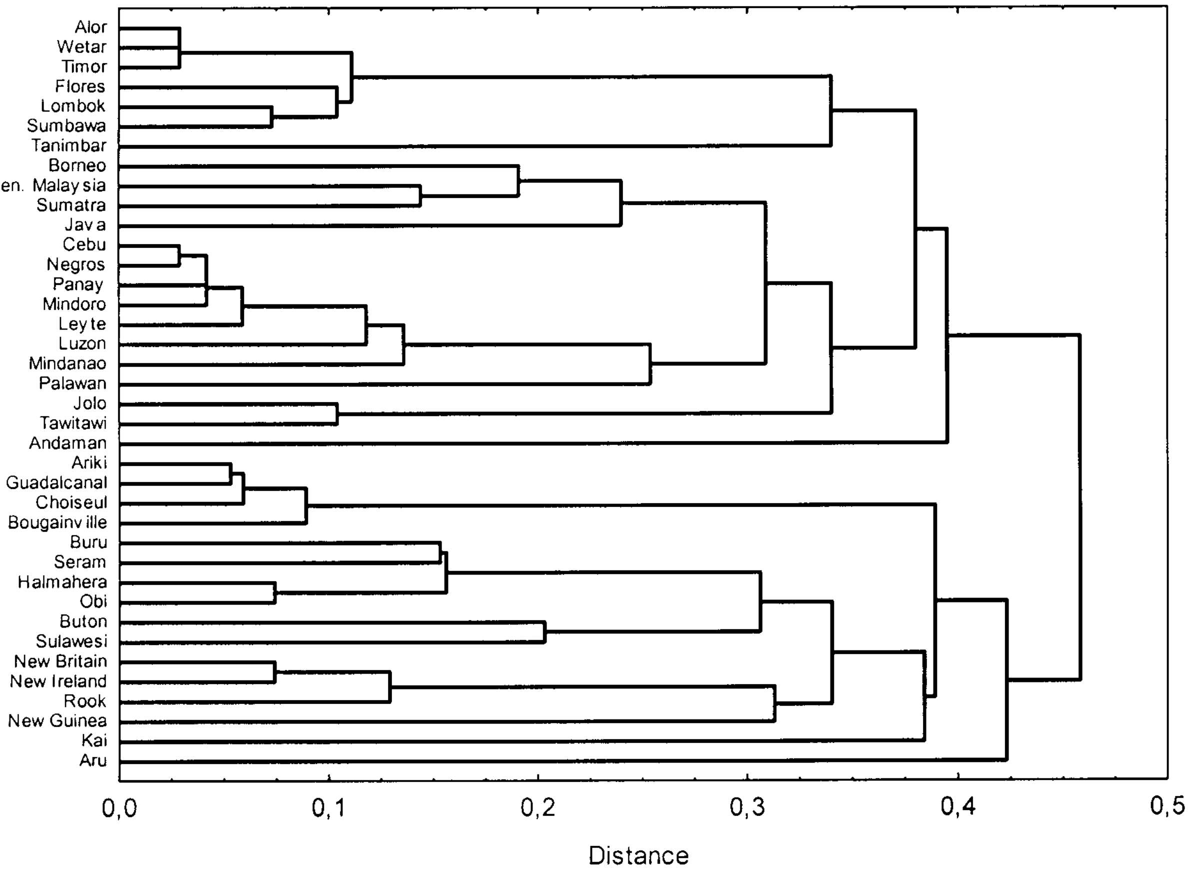


Figure 4.5 shows the biogeographical associations of Sphingidae in the Malesian archipelago (single-linkage cluster analysis for 38 islands, based on Preston's (1962b) coefficients). The following islands have nested faunas (i.e., they are fully contained in bold-printed island) and were excluded from analysis (see text):

Andaman: Nicobar **Ariki**: Kolombangara, New Georgia, Rendova, Vella Lavella **Borneo**: Natuna **Bougainville**: Alu **Flores**: Adonara, Lembata ('Solor archipelago') **Guadalcanal**: Florida, Isabel, Makira, Malaita, Rennel, San Jorge, Santa Cruz **Halmahera**: Bacan, Gebi **Java**: Bali **Leyte**: Dinagat, Homohon, Panaon, Taytay, Samar **Luzon**: Burias, Camiguin de Luzon, Catanduanes, Marinduque, Masbate, Polillo, Ticao **Mindanao**: Basilan, Camiguin de Mindanao, Calayan **Mindoro**: Sibuyan **Negros**: Bohol, Siquijor **New Guinea**: Biak, Dampier, Ferguson, Goodenough, Mefor, Misol, Rossel, St. Aignan, Sudest, Trobriand, Waigeo, Woodlark **New Ireland**: Dyaul, Lavongai, Manus, Mussau **Palawan**: Balabac, Calamian, Dumaran **Seram**: Ambon, Kelang **Sulawesi**: Sangir, Selayer, Sula **Sumatra**: Banka, Sabang, Nias, Simeuloe, Pagai-Pagai, Pini, Mentawi **Sumbawa**: Sumba, Komodo **Tanimbar**: Yamdena, Selaru, Larat ('Tanimbar islands') **Timor**: Damar, Leti, Roma, Sermatta ('Bandar Daya islands')

2) Phenetic classification of regions

In figure 4.5 a classification of islands by their faunal similarity is displayed, figure 4.6 shows the associated linkage diagram. The dendrogram yields surprisingly clear and interpretable patterns: 'Wallace's line' (see Monk et al. 1997) appears as the main faunal discontinuity in the region, only the Tanimbar islands do not fit this 'classical' pattern but are loosely associated with the Western (instead of the Eastern) part of the archipelago. The Western sub-region falls into four main blocks: (1) The Sundaland area (except Palawan) is clustering together, with Java slightly more separate from the other main islands. Sundaland islands share a high biological similarity in many groups of organisms (e.g. Withmore 1981, 1987) as they formed a continuous land mass during eras of lower water levels (Voris 2000). (2) The Philippine main islands are grouped closely together, whereas Palawan (which is grouped with Sundaland for many other taxa, Withmore 1987, see also Voris 2000) is only loosely associated with the other islands. (3) The 'Sulu archipelago' (Jolo, Tawitawi) in the South-Eastern Philippines has a quite distinct fauna that is well separated from the rest of the Philippines, Borneo or Sulawesi. (4) The Lesser Sunda Islands form a tight, separate block within the Western sub-region (see also Holloway 1987b), while the Andaman Islands are very isolated and only loosely associated with the rest of the archipelago. In the Eastern sub-region, (1) the Solomon Islands (including Bougainville) are a clearly separated archipelago, as are (2) the Bismarck Islands. New Guinea appears to house a quite isolated fauna, which is probably due to a high degree of endemics (table 4.2). (3) The Moluccas (except the Southern island groups Aru, Tanimbar & Kai) form an own block, which falls into a Northern and a

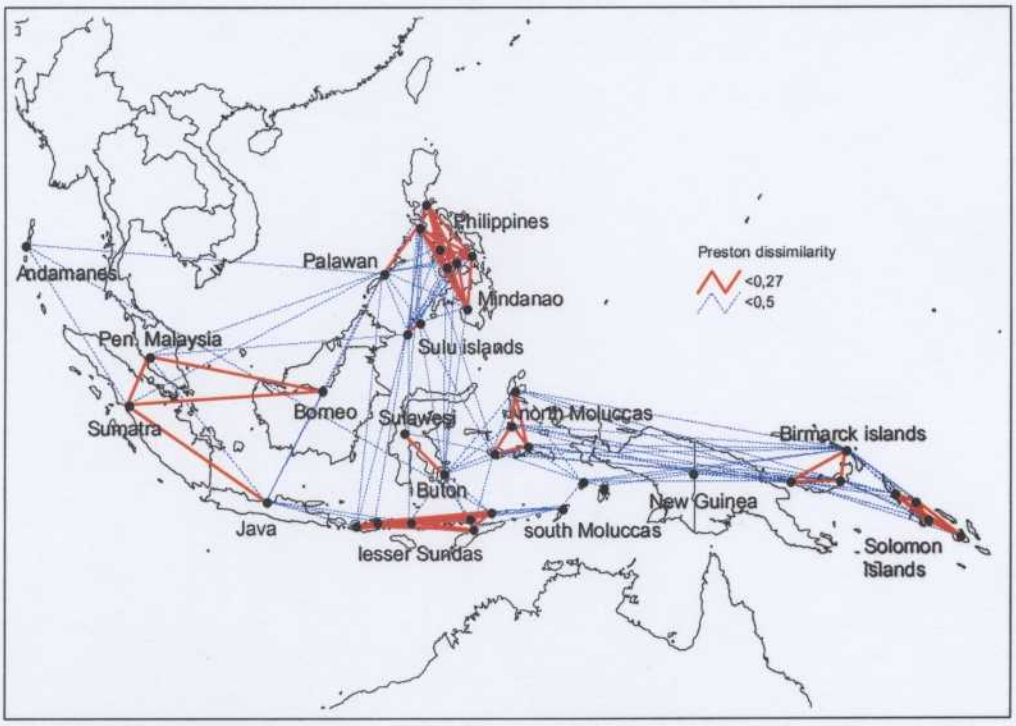


Figure 4.6 shows a linkage diagram of Sphingidae faunas based on Preston's coefficient (see figure 4.5). For easier geographic association, islands in the diagram are displayed on their geographical position in a map of SE-Asia. Preston coefficients >0,27 indicate that "there is, and has long been, some degree of genuine isolation" between regions (Preston 1962).

Southern part, while (4) Sulawesi is closely associated only with Buton Island. In contrast to Holloway's (1987b) assessment (based on phenetic analyses as well as area-cladograms from allopatric species arrays) 'Wallacea' and 'Melanesia' (from the Moluccas to the Solomon Islands) appear as quite heterogeneous regions for Sphingidae. The geographically isolated Kai and Aru islands have, similarly as 'nearby' Tanimbar, relatively isolated faunas within their sub-region, but only on the latter island group endemic hawkmoth species are known (table 4.2).

A comparison with a cluster analysis based on Bray-Curtis similarities (e.g. Southwood & Henderson 2000; data is not shown, but may be viewed in Beck & Kitching 2004) confirms most, but not all of the observed patterns: The Lesser Sunda Islands are grouped with the Eastern rather than the Western sub-region, which indicates that these islands are a transition zone between the East and the West. Similarly, Palawan is grouped with Sundaland rather than the Philippine main group, which also shows the transitionary character of this island's fauna. An analysis of Sørensen indices in combination with MDS (data are not shown, but can be viewed in Beck & Kitching 2004) confirms this judgement. The idea that Weber's line (between Sulawesi and the Moluccas, Monk et al. 1997) is the main faunal discontinuity for hawkmoths in the region (as for some other Lepidoptera groups, Holloway 1987b) is not supported by these data.

Region	Endemics*)	Species (total)	%Endemics
Andamanes	1	36	*2,8*
Sundaland)**	**34**	**164**	***20,7***
Borneo	2	113	*1,8*
Java	0	109	*0,0*
Palawan	0	89	*0,0*
Sumatra	2	127	*1,6*
Lesser Sundas	**6**	**55**	***10,9***
Western less. Sund (NTB)	2	51	*3,9*
Easter less. Sund. (NTT)	3	49	*6,1*
Wallacea	**23**	**140**	***16,4***
Luzon	1	87	*1,1*
Mindanao	2	82	*2,4*
Sulawesi	19	84	*22,6*
Sulu islands	1	39	*2,6*
Moluccas	**12**	**79**	***15,2***
north	7	59	*11,9*
Kai	0	26	*0,0*
Aru	0	21	*0,0*
Tanimbar	4	37	*10,8*
New Guinea	**21**	**78**	***26,9***
Bismarck islands	**6**	**43**	***14,0***
New Britain	1	41	*2,4*
New Ireland	1	38	*2,6*
Solomon islands	**2**	**28**	***7,1***
Bougainville	1	32	*3,1*
Guadalcanal	1	32	*3,1*

*) includes nested island faunas

**) Sundaland "endemics" refers to species which are not found in other parts of the Archipelago, but many stretch into continental SE-Asia.

Table 4.2 shows degrees of endemism in the major regions as well as some single islands of the Malesian archipelago.

In order to explore these patterns for statistical significant groupings, permutation tests were conducted for several hypothetical faunal boundaries. An 'Analysis of Similarities' (ANOSIM, 10.000 randomisation of the Preston-similarity matrix, using the computer program *PRIMER 5* (2002)) reveals significant effects of *a)* Wallace's line ($R_{global}=0,681$, $p<0,001$), *b)* regions according to Holloway (1987b, Sundaland, Wallacea, Lesser Sundas, Melanesia: $R_{global}=0,625$, $p<0,001$, all pair-wise comparisons significant), and *c)* a grouping according to figure 4.5 at a distance of z=0,27 (see also figure 4.6: $R_{global}=0,987$, $p<0,001$). In the latter test, some non-significant pair-wise comparisons occur but relate to groups with only one or few islands, hence to comparisons with a low statistical power. Interesting pair-wise test results are a clear separation within 'Wallacea' (*Sulawesi-group:Philippine-group*, *Philippine-group:Sulu archipelago*, both p=0,022).

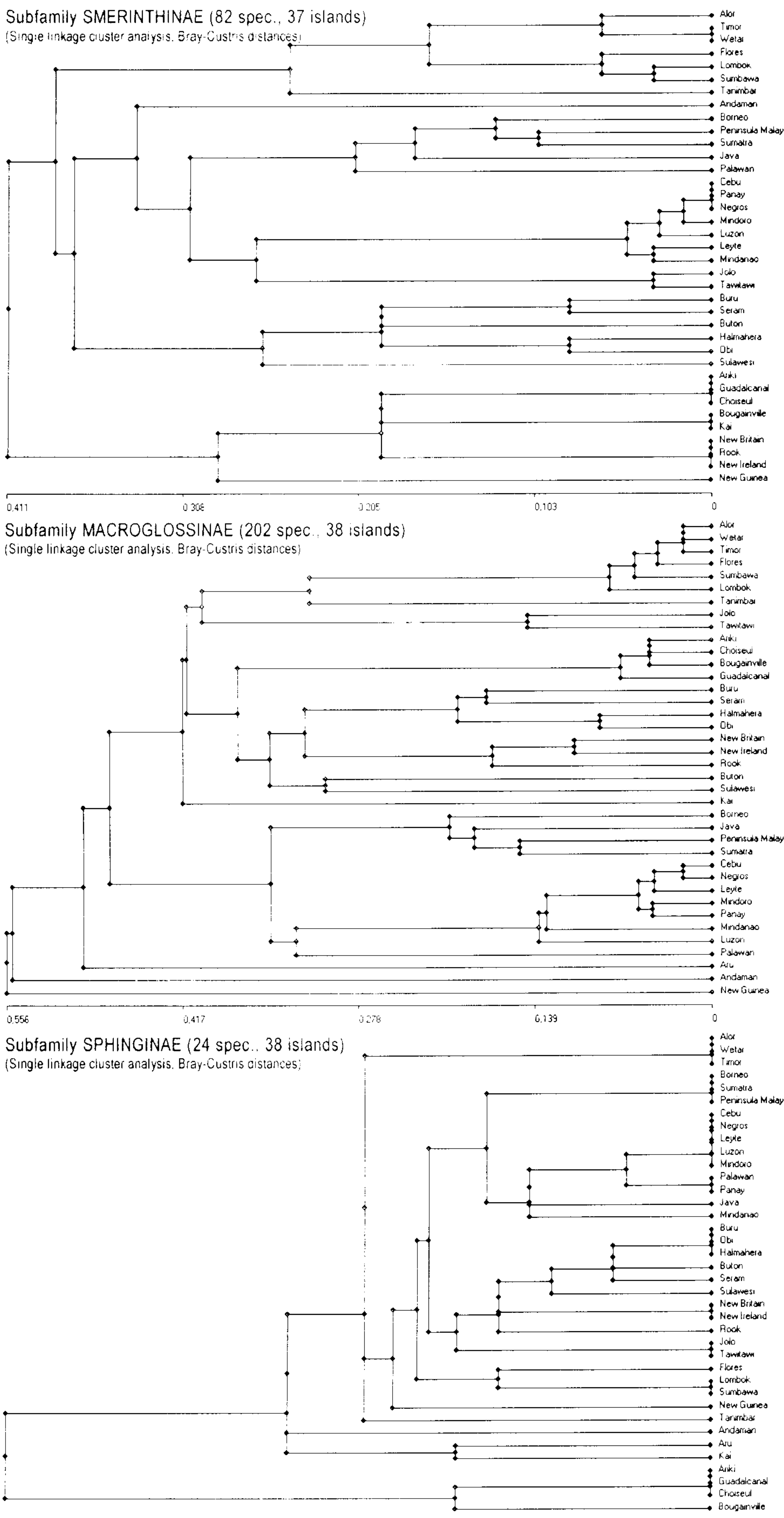
Table 4.2 gives figures for the degree of species endemism of the main regions as well as some selected islands. A relatively high degree of endemism justifies the separation of all major regions from each other. However, a high endemism of some islands or island groups within major regions indicates a high degree of isolation. Particularly in the case of the 22 percent endemics in Sulawesi a grouping with the Philippines as 'Wallacea' seems questionable. However, it has been suggested that the habit of Sphingidae taxonomists to separate specimens from the Philippines and Sulawesi into 'good', albeit very similar species might be partly responsible for this pattern (I.J. Kitching pers. com).

Separate cluster analyses for the subfamilies (based on Bray-Curtis coefficients for easier computation) shows mostly the same patterns as for the whole family as far as sub-groups of similar island groups are concerned (figure 4.7). However, the arrangements of these sub-groups to each other differs between subfamilies, and particularly for the Smerinthinae distance measures between subgroups are considerably larger than for other subfamilies. For Smerinthinae, Lydekker's line between the Moluccas and New Guinea (see Monk et al. 1997) appears as the major faunal discontinuity in the region. Noteworthy is also the huge separation between the Solomon Islands and the rest of the archipelago in Sphinginae, a pattern that was not observed for other subfamilies.

3) Patterns and processes within 'homogenous' faunal regions

Several relatively 'homogenous' areas can be identified in figure 4.5 & 4.6: The Sundaland area (except Palawan), the Lesser Sundas, the Philippines (except the Sulu archipelago, and with questionable Palawan & nested islands), the Sulawesi-group, the Moluccas (except Tanimbar, Kai & Aru), New Guinea and surrounding islands, the Bismarck archipelago, and the Solomon Islands. A fair degree of faunal exchange probably occurs within these areas (Preston 1962). Many of the regions were connected to each other during times of lower sea levels (Voris 2000), while the Moluccas are a geologically heterogeneous region in an area of relatively deep sea (Hall 1998, de Jong 1998).

Atmar & Patterson (1993) suggested that under the assumptions of (1) a fragmented habitat that was once whole and originally populated by a single common source biota, (2) islands that were initially uniform in their habitat heterogeneity, and have remained so throughout their post-fragmentation history, (3) no significant clinal gradation, and (4) equal isolation of all species on all islands, extinction in habitat fragments of different size follows a regularity that leads to non-random distributions of species over such fragments. A measure of the 'predictability' of such nested island faunas was termed 'temperature' and ranges from zero to 100 degrees (Atmar & Patterson 1993, 1995). Whereas random variation of stochastic environmental, demographic, genetic, and catastrophic events lead to a general rise in 'temperature' of a island-species matrix of nested faunas, habitat heterogeneity or



Subfamily SMERINTHINAE (82 spec., 37 islands)
(Single linkage cluster analysis. Bray-Custris distances)

Subfamily MACROGLOSSINAE (202 spec., 38 islands)
(Single linkage cluster analysis. Bray-Custris distances)

Subfamily SPHINGINAE (24 spec., 38 islands)
(Single linkage cluster analysis. Bray-Custris distances)

Figure 4.7 shows the biogeographical associations of the three subfamilies of hawkmoths in Malesia (see text for details, figure 4.5 for nested island faunas).

Region	**Islands**	**Species**	**Spec. on all isl.**	**T_{matrix} [°]**	**Matrix fill [%]**	**Random matrix : T_{mean}±SD [°]**	**Idiosyncratic species: $T_{spec}>2*T_{matrix}$**	**Idiosyncratic islands: $T_{isl}>2*T_{matrix}$**
Sundaland	12	156	6	14,31	41,7	64,6±2,6	21 (*14,0%*)	1 (*8,3%*)
Lesser Sundas	14	55	9	13,16	59,9	62,1±4,4	11 (*23,9%*)	1 (*7,1%*)
Philippines	27	126	17	25,92	51,0	73,8±1,9	12 (11,0%)	3 (*11,1%*)
Phil. (expt. Palawan)	23	126	26	19,30	61,3	69,9±2,8	16 (*16,0%*)	3 (*13,0%*)
Sulawesi-group	5	85	5	2,32	42,0	46,8±5,5	3 (*3,8%*)	1 (*20,0%*)
Moluccas	8	59	10	16,16	62,2	55,1±5,6	6 (*12,2%*)	1 (*12,5%*)
New Guinea	13	78	7	10,43	43,4	62,9±3,4	11 (*15,5%*)	1 (*7,7%*)
Bismarcks	7	43	8	4,59	58,7	52,2±6,6	4 (*11,4%*)	1 (*14,3%*)
Solomons	11	33	0	3,97	77,4	41,2±6,6	4 (*12,1%*)	1 (*9,1%*)

Table 4.3 shows the 'matrix temperature' T (Atmar & Patterson 1993, 1995) of faunal lists for biogeographically homogenous archipelagos (Preston distances <0,27, & nested islands; see figure 4.5 & 4.6). Matrix temperature, matrix fills and percentage values for idiosyncratic species and islands were calculated for maximally packed matrices, which excludes species that occur on all islands. Mean temperatures for random matrices stem from a Monte Carlo simulation (500 runs, Atmar & Patterson 1995).

biogeographic effects let single species or island exhibit a considerably higher 'temperature' than the matrix in which they are imbedded. Such violations of the assumptions from the model-process of habitat fragmentation lead to idiosyncrasies in species distribution that can be distinguished from random noise in data (Atmar & Patterson 1993). Nestedness of species assemblages is a sign for consistent differences in immigration and extinction of species. It is negatively related to β-diversity and has been advocated as a tool for optimising conservation reserve planning (Wright & Reeves 1992),

Table 4.3 shows 'matrix temperatures' for the main regions (calculated with the computer program *Nestedness Temperature Calculator*, Atmar & Patterson 1995). Temperature varies considerably among regions: It is low in the Bismarck and Solomon Islands as well as on the Sulawesi-group, very high in the Philippines if the Palawan-group is included and intermediate in the other regions. All matrix temperatures are significantly lower than in a randomly generated matrix of equal fill ($p<10^{-8}$, MC-simulation, 500 runs). Low temperatures indicate a higher than random order of island faunas, while higher than random temperatures would indicate non-random heterogeneity that could be caused by competitive exclusion (i.e. 'checkerspot distributions', Diamond 1975) or allopatric speciation (Atmar & Patterson 1993).

While it would lead too far here to identify species or islands with temperatures higher that their island-species matrix and to search for ecological or historical reasons for this deviation, a comparison of the proportional occurrence of such events might lead to further understanding of the fauna of the archipelago (see table 4.3; counted are species with temperatures double the matrix temperature or larger). Deviations of island temperatures are very difficult to interpret (Atmar & Patterson 1993) and will not be treated further here. The percentage of idiosyncratic species distributions is low in the Sulawesi group, which is thus identified as a largely 'nested' archipelago. Surprisingly it is considerably higher in the 'New Guinea-group', although all the islands have faunas which are nested within that of New Guinea (see figure 4.5). Idiosyncrasies here are probably caused by the huge size differences of islands (see e.g. figure 4.1b) as well as the altitudinal zonation of New Guinea, which give this island a large proportion of restricted species that are completely absent from the other islands (see also table 4.2). Despite apparent congruency of the geological history of Sundaland and the Philippines with Atmar & Patterson's (1993) habitat fragmentation model (due to varying sea levels, Voris 2000), the proportion of idiosyncratic species distribution is not particularly low in these regions, while it is not obviously higher in the geologically divers Moluccas. The region with the highest proportion of deviant species 'temperatures' is the Lesser Sunda chain. In this island group climatic variation (especially in precipitation, Monk et al. 1997) might be responsible for this effect. Furthermore, the East-West orientation of the island chain, with immigration possibilities mainly either from the one or the other end (Monk et al. 1997), might lead to clinal gradients (see also the separation into an Eastern and a Western part, figure 4.5).

4) Correlations with faunal similarity: Modern-day distance or ancient land blocks?

To test the influence of distance and land-units during lower sea levels, partial Mantel tests (Legendre 1993, Legendre & Legendre 1998, computed with *IBD 1.5*, Bohonak 2002) were applied to faunal similarities (Preston coefficients) for the non-nested islands (see figure 4.5). Geographical distances between island centroids were calculated from latitude and longitude data (using geodesic correction, *ArcView 3.2* 2000). As a second predictor, a binary matrix for unified land areas during lower sea levels was assembled from both the 50 metres and the 100 metres contour maps in Voris (2000). During the last 17.000 years, sea levels in Southeast-Asia dropped for 7.000 years as low as or lower than 50 metres and for 4.000 years as low as or lower than 100 metres below today's coastline (Voris 2000). The Bismarck and Solomon Islands are not included in Voris' (2000) maps, so only 31 island faunas could be tested. All tested variables are significantly correlated with faunal similarity, independently as well as in partial tests (see table 4.4. for test results). The logarithm of geographic distance alone is a significant predictor of faunal similarity variation and does not loose much explanation power if controlled for sea-level caused blocks of unified land masses. Land unity has significant, yet lower R-values, but the latter might not mean much as the binary data structure is much coarser than for distance.

Mantel Test Statistics:	*50 metres contour*			*100 metres contour*		
Correlation of **faunal similarity** with	Z	r	p	Z	r	p
Log(**geogr. distance**) [m]	1530,5	0,773	<0,001	1530,5	0,773	<0,001
Land unity [binary code]	241,7	0,571	<0,001	228,5	0,546	<0,001
Log(**geogr. distance**) – **partial** (controlled for land unity)		0,720	<0,001		0,714	<0,001
Land unity – partial (controlled for geogr. distance)		0,439	<0,001		0,381	<0,001

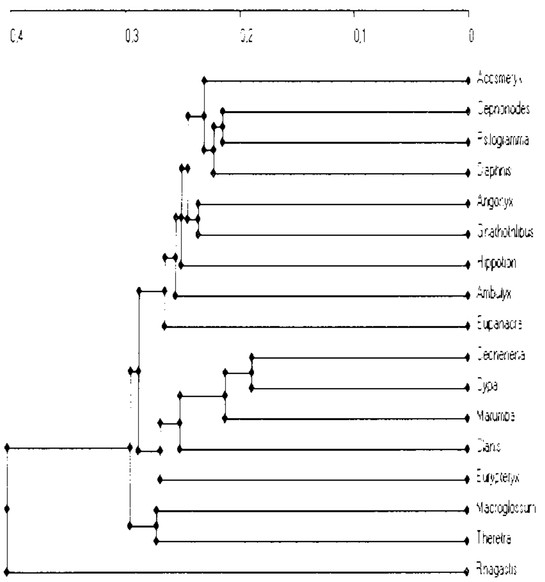
Table 4.4 shows test results from partial Mantel-tests of 31 faunal similarities with geographic distance and land-units at sea levels 50 meters and 100 meters below today's (*IBD 1.5*, Bohonak 2002, 1000 randomizations).

5) R-mode analysis

As an alternative to phenetic analyses of islands similarity, r-mode clustering of groups of species with similar distribution was suggested (Holloway 1998b). Such groups can be a starting point for cladistic approaches to biogeographical patterns (Holloway 1998b). A simple r-mode analysis, classifying 308 species according to their distribution on 38 islands was conducted. Based on Bray-Curtis coefficients, single linkage cluster analysis yields groupings which are only in parts well interpretable. Complete linkage clustering yields a slightly better grouping, but groups still occasionally contain species with deviating distribution patterns. It would be inconvenient to show data here due to the size of the dendrogram, but it can be viewed in Beck & Kitching (2004).

For further exploration, the more sophisticated r-mode analysis method suggested by Holloway (1998b) was applied in a slightly modified way: For 17 genera with more than five species in the region, the number of species in the 14 (non-nested) biogeographical regions of the Malesian archipelago was analysed (see table in figure 4.8). However, as the r-mode classification of species did not lead to satisfyingly defined groups of species with similar geographical range (see r-mode cluster analysis in Beck & Kitching 2004), the classification was based on the phenetic q-mode analysis presented in figure 4.5 & 4.6. A single link cluster analysis of Bray-Curtis indices from this data ordered genera according to similarities in distribution as well as their faunal centres (figure 4.8).

The genera in analysis showed well-defined differences in distribution and species richness in different regions, but a comparison with the input data makes it not easy to pinpoint these differences to distribution patterns. To aid this interpretation process, a detrended correspondence analysis (DECORONA, calculated with *Community Analysis Package 2.04*, Henderson & Seaby 2002) of the same data was used. In DECORONA-plots genera and regions are ordinated along the same axes, which show associations more clearly than the raw data in figure 4.8. On plots of the two major axes (not shown) the following distributions centres were identified, which can be confirmed easily, in retrospect, from the data in figure 4.8 (starting at the bottom of the dendrogram): (1) *Rhagastis* is an oriental genus that penetrates not far beyond Sundaland into the archipelago. (2) *Theretra* & *Macroglossum* are widespread, almost ubiquitous genera. Both are relatively large (e.g. *Macroglossum*: 73 species), so a finer taxonomic resolution might yield more information from their distribution (see Holloway 1998b). (3) *Marumba, Clanis, Cechenena & Cypa* are genera which have their centres of distribution west of the Wallace line, while loosely associated *Eurypteryx* is centred more transitory between the Philippines, Sulawesi & the Moluccas. (4) The remaining cluster involves genera which are all widespread throughout the archipelago, but with a distinctively more eastern centre than the above mentioned genera. Of these, the distribution centres of *Acosmeryx & Ambulyx* might still be considered transitory between the Sundaland-Philippine and the Moluccan-New Guinean region, while the remaining genera are clearly centred East of the Wallace line, though not further East than New Guinea.



	Andaman	Sundaland*)	Palawan	Lesser Sunda	Philippines**)	Sulu-isl.	Sulawesi-group	Moluccas (north)	Kai	Aru	Tanimbar	New Guinea	Bismarcks	Solomons
Acosmeryx	1	4	2	2	2	2	1	1	1	1	1	2	2	
Cephonodes	2	2	2	3	3	1	4	2			1	3	1	2
Psilogramma	2	3	2	4	2	1	2	2	1	1	2	4	3	1
Daphnis	2	3	3	2	4	3	4	3	3	1	2	4	4	4
Angonyx	1	1	1	1	1	1	1	1			1	2	2	2
Gnathothlibus	1	2	1	1	1		3	1	1	1	1	3	1	2
Hippotion	2	7	5	6	7	3	6	7	3	3	5	7	5	4
Ambulyx	3	9	7	4	8	6	4	5	1		1	4	2	2
Eupanacra	2	11	5	2	6		5	1	1	1		3	1	1
Cechenena		5	4	1	2	1	2	1				1	1	
Cypa		5	1		2	1	2	1				2		
Marumba	1	7	3	2	2	1	2	1			1			
Clanis	1	4	1	1	2		1	1			1			
Eurypteryx		3	2		3		2	3			1	2		
Macroglossum	5	31	21	7	27	5	20	10	5	6	10	22	7	11
Theretra	5	14	10	11	11	7	10	11	8	6	8	11	10	6
Rhagastis		5	1											

Figure 4.8 shows an r-mode cluster analysis (single linkage, Bray-Curtis similarities) of Sphingid genera according to their distribution and faunal centres (Holloway 1998b). The table on the right gives data on species numbers of the respective genera in the faunal regions. See text for further details and interpretation.*) 'Sundaland' excludes Palawan **) 'Philippines' excludes the Sulu islands and Palawan.

Discussion

Biases and circularities in range estimates

Estimating species ranges from recorded data is an essential prerequisite for almost all analyses of distribution patterns. Leaving aside the very few really well-sampled organisms (e.g. British birds: BirdLife International/European Bird Census Council 2000), the geographic ranges of most organism have to be assessed from more or less scattered records. Decisions on the procedure and scale of this assessment are often governed by data availability. For example, presence-absence measurement of species in 100 km^2-grid cells is an option for British butterflies (see Quinn et al. 1996), but not for those in New Guinea. Such differences can strongly influence methods and results of analyses (e.g. Graham et al. 2004; see Burrough 1981, Bolliger et al. 2003 for the fractal nature of environmental data). GIS modelling, including the related field of remote sensing, is an increasingly powerful aid to make such estimates more reliable and fine-grained (e.g. Segurado & Araujo 2004, Guisan et al. 2002, Ziv 1998, Gustavson et al. 2001, Lehmann et al. 2003, Zaniewski et al. 2002, Mackey & Lindenmayer 2001, Cowley et al. 2000, Ray et al. 2002). However, a model is only as good as its underlying assumptions and the quality of reference data. No matter if a computerised algorithm (e.g. Raxworthy et al. 2003) or a 'human controlled' approach (as in this study) is used to imply the assumptions on species ranges, artefacts in distribution patterns can be created that cause circularity: Assumptions about distribution patterns will be proven in the consequent data analysis. As recorded data is not a reasonable option for tropical invertebrates due to obvious undersampling effects (see above), potentially biased results must be accepted yet carefully discussed and, if possible, confirmed by independent analyses in order to be correctly interpreted (see Lawton 2000).

Geographical and climatological information were important predictors of species' global ranges, but climate and vegetation are relatively uniform within Malesia, which is the focus of the biogeographical analyses in this study. Despite the application of a quite conservative approach (see above) that did not transgress boundaries of geographically clustered island groups without proving record, two main assumptions might have led to artefacts: (1) While species with restricted range records were treated very conservatively, this was not done with species with very widespread and dense records in all well-sampled regions. On the contrary, it was assumed that such species with high dispersal abilities (and sometimes pan-tropical distributions, e.g. *Agrius convolvuli*) have reached even relatively remote, undersampled regions and particularly small islands nearby larger islands with positive records. A further argument in favour of this procedure was the likelihood that such common species might have been found but not sampled and recorded as they are nothing special for taxonomists and hobby collectors (see also Graham et al. 2004). However, the arbitrary choice of included islands might have artificially inflated the estimated species richness of some small islands. The flat species-area relationship and high variability of species richness for smaller islands (see figure 4.1) might have been partly produced by this artefact, but the generally low slope in this part of the species-area relation was also observed for recorded island faunas. (2) Geographically dense archipelagos were often treated as one 'unit', where a positive record on some islands indicated occurrence on all islands. This applied particularly to badly sampled islands and to species which are hard to find (e.g. because they do not come to artificial light sources) or which are easily misidentified and confused with a commonly reported species. The high faunal similarity of the Philippine main group and of the Solomon Islands might have been artificially inflated by this procedure.

Is hawkmoth distribution shaped by dispersal or past geography?

Geological history and particularly changes in sea level have led to idiosyncratic species distributions in the Malesian archipelago for many taxa (e.g. Hall & Holloway 1998, Whitmore 1987, see also Jansson 2003 for other regions) and could also be observed for Sphingidae in this study. Patterns such as the unity of Sundaland and the central Philipppine islands, as well as their connection through transitory Palawan, or the similarity of Sulawesi and New Guinea with their surrounding islands, respectively, can be readily explained by lower sea levels (Voris 2000), which unified these areas yet left separating deep sea zones as well as unsuitable habitat due to climatic changes between them (e.g. Brandon-Jones 1998, Gathorne-Hardy et al. 2002b, see also vegetation maps in Picket et al. 2004). Subsequent raise in sea levels caused vicariance within the land blocks and led to ordered extinctions on the smaller islands which were disturbed by random events (Atmer & Patterson 1993, 'ecological release' *sensu* Diamond 1972, 1975). Other island groups, however, do not share such a history: The Moluccas, for example, are a geologically divers region that has never been a connected block of land (Hall 1998, Metcalfe 1998). Consequently, different distributions patterns and a generally higher heterogeneity than within island groups such as Sundaland should be expected within the Moluccan region (see e.g. de Jong 1998 for butterflies), if geographical history was the major determinant of species distribution.

Tight matches between species distribution and geological history have frequently be observed even within composite islands (such as New Zealand, Sulawesi; e.g. Musser 1987) and are even suspected for some Sphingidae species on Taiwan and New Guinea (see maps in Beck & Kitching 2004). Such correlations are not necessarily a proof for the 'rafting' of species on tectonic fragments without subsequent dispersal (e.g. Musser 1987), but could also be mediated by habitat differences in the present that could be ultimately caused by tectonic events. As an obvious example, human settlers of Austronesian ('Malayan') decent settled on the north coast of New Guinea in prehistoric times, while they did not penetrate into the (tectonically different) central highlands and southern swamps of the island, which until now are predominantly populated by people of Papuan ethnics (Diamond 1998). However, Sphingid faunas in a region with a homogenous history like Sundaland do not have a higher similarity than the 'composite' archipelago of the Moluccas (see figure 4.5; mean Preston-coefficient [±SD], Sundaland: 0,25±0,08; Moluccas: 0,26±0,18). Furthermore, a nestedness analysis of matrix temperatures (see table 4.3) indicated similar portions of idiosyncratic species distributions in geologically homogenous and heterogenous regions. The Lesser Sunda Islands, which were never completely connected to each other even during low sea levels (Voris 2000), seem to match predictions for a heterogenous history with their high proportion of idiosyncratic species (table 4.3), but this might also have been caused by their present climatic heterogeneity or their geographic chain shape (Monk et al. 1997), as outlined above.

While large-scale patterns with a geological basis are still clearly present in Sphingid distribution (figure 4.6) and patterns of endemism (table 4.2), the above results lead to the interpretation that dispersal has influenced the island groups so heavily that differences between regions of sea-level caused vicariance and areas of genuine geological heterogeneity are blurred beyond recognition.

Partial Mantel tests confirm that both distance and land unity have a significant influence on Sphingid distribution. Sea level maps at 50 metres below today are better predictors of faunal similarity than those for 100 metres. However, it remains unclear in what time-frame the distribution of hawkmoths over Southeast-Asia happened. It must be expected that different phylogenetic lineages might have dispersed and speciated at very different times and thus under different geographical conditions, which might be reflected for example in the different biogeographic patterns of the three subfamilies (figure 4.7). The oldest fossilised specimen that could plausibly be associated with the Sphingidae is *Mioclanis shanwangiana* from Shandong province, China, which is of Miocene age (I.J. Kitching, pers.com.). If the taxonomic affiliation of the moth (which is by far not confirmed) was accepted, at least some Sphingidae lineages were probably spread over Southeast-Asia during a much longer time period than the most recent, late Pleistocene changes in climate and sea-level, which considerably complicates the understanding of what caused present day distribution patterns. A cladistic analysis of the biogeograpahic patterns of Sphingidae lineages of different evolutionary age as well as comparisons to other Lepidoptera taxa (such a Saturniidae) might help to understand such questions, but would, as a first step, require a reasonable hypothesis on the phylogeny of the taxa (see also Barraclough & Vogler 2000).

Sphingidae are fairly generalist feeders (Robinson et al. 2001a, b, see also chapter 5.1) and very well flying insects (chapter 2) with tendencies for migration in some taxa. Furthermore, at least one subfamily seems not to be bound to ecologically stable, undisturbed habitats in Southeast-Asia (chapter 3.1). All these factors make it likely that Sphingidae are extraordinarily good dispersers (compare e.g. to Wilson 1961), and many species have very large ranges (chapter 4.2). Lacks in comparable data quality of distribution records as well as taxonomy make it difficult to compare Sphingid range sizes to other Lepidoptera groups in Southeast-Asia, but a comparison of European distributions (from country lists in Karsholt & Razowski 1996, multiplied with area size for countries) shows much larger (partial) ranges for European Sphingidae than for European Papilionoidea, Geometridae, Noctuidea or all Lepidoptera (KW-Anova, N=8.459, $H_{df=4}=78{,}6$, $p<0{,}0001$). Thus, it is not surprising that dispersal between islands occurs regularly and plays an important role in Sphingid distribution in the Malesian region.

Dispersal and life-history strategies

Two hypotheses were suggested of how distribution patterns might differ between subfamilies. However, no effect of rainforest blocks on islands, which was expected because of a higher frequency of Smerinthinae in primary forests on Borneo (see chapter 3.1) was found. Rainforests, as well as island area, appear to be correlates of geographic position without any independent influence on subfamily distributions. Smerinthinae are weaker dispersers than the two other subfamilies, as could be shown from a steeper distance-turnover relation (figure 4.4). The effect of geographic position (latitude, longitude) is most likely the consequence of distance to continental Asia (which is most probably the main source area for immigration), while it remains unclear if the dispersal abilities of Smerinthinae are inferior because they cannot reach the islands, e.g. because of weaker flight abilities (lower 'wing load', chapter 5.2), females with heavy egg-loads in their abdomen (which has a negative effect on flight performance, see e.g. Didley 1995) or shorter adult life span caused by a *capital breeding* life history (see Tammaru & Haukioja 1996 and references therein). The latter is evident in the tribus Smerinthini (Kitching & Cadiou 2000), but not in the Ambulycini, which nevertheless show a steep faunal turnover (figure 4.4). Alternatively, Smerinthinae may not easily establish on new sites, e.g. because of a higher host plant specialisation (chapter 5.1). However, a 'quick and dirty' analysis of larval host plant distributions (on plant family level), which is presented in more detail in chapter 5.1, suggests that the limits of species ranges in the Malesian archipelago are not determined by those of the host plant families. Usually, host plant ranges appear to be considerably larger than moth ranges, which is congruent with the results of Quinn et al. (1997, 1998) on British Lepidoptera.

Generalized Linear Models were successfully used in spatial analyses of species distribution (Guisan et al. 2002, Rushton et al. 2004) and results of the GLM-analysis are not unreasonable (see paragraph above), but still have to be viewed with care as such multivariate approaches generally carry a danger of confusing best-fitting functions and causal explanations due to collinearity of predictor variables (McNally 2000). However, the ecologically reasonable choice of relatively few (four) predictor variables in comparison to sample sizes is probably keeping this danger low in the present data set (McNally 2000); the same reasoning applies to the GLM analysis of absolute species richness.

In conclusion, it appears that differences in dispersal ability between subfamilies are mainly responsible for differences in their respective distribution. It is not unlikely that these differences were caused by different life history strategies (Begon et al. 1996), i.e. the distinction between *income breeding* and *capital breeding* groups in the Sphingidae (Lemaire & Minet 1998), which also might have consequences on frequencies in local habitats (chapter 3.1), but further investigation will be needed to categorise the life history of the tribus Ambulycini that shows distribution patterns as the *capital breeding* Smerinthini, although its species were shown to feed on flowers as adults (see also chapter 1.2 & 7). Difference in species' abilities to reach and persist on islands were recently put forward (Lomolino 2000, see also Diamond 1975) as a model to explain patterns of island biogeography, alternative to McArthur & Wilson's classical equilibrium model (see e.g. Whittaker 1998 for review and discussion). It remains to be seen in further analyses if hawkmoth data support predictions from this approach on a species level.

Allopatric speciation is to a large extent dependent on the isolation of populations or founder individuals (e.g. Mayr 1963). Therefore, lower dispersal abilities should, everything else being equal, lead to higher speciation rates. Speciation patterns were not explicitly addressed in this study (partly because of the unresolved phylogenies in many groups), but as a first assessment the proportions of Smerinthinae *vs.* the two other subfamilies could be compared between complete (estimated) island faunas and the endemic portion of the respective islands. For three island faunas with a relatively high proportion of endemics (see table 4.2), contingency tables did not reveal significant differences in proportions, which would indicate different speciation rates between the two life history types, although Sulawesi data show a strong trend (New Guinea: $\chi^2_{df=1}=0{,}30$, $p_{one\text{-}sided}=0{,}292$; Sulawesi: $\chi^2_{df=1}=2{,}39$, $p_{one\text{-}sided}=0{,}061$; Tanimbar: $\chi^2_{df=1}=0{,}35$, $p_{one\text{-}sided}=0{,}277$).

The correlations of life history traits such as adult resource allocation, (suspected) adult longevity, niche breadth (chapter 5.1) and sexual dimorphism with patterns of distribution and dispersal (see above), range size (chapter 4.2) and local habitat (chapter 3.1; see also Southwood 1988) matches results on other Lepidoptera in the tropics (Braby 2002 and references therein, Janzen 1984) as well as in temperate regions (e.g. Brändle 2002b). Its consequences on macroecological patterns will be further explored in chapter 6.

CHAPTER 4.2 - RANGE SIZE MEASUREMENTS

Abstract

Different measurements of the geographic range size of Southeast-Asian Sphingidae were compared with respect to the resolution and geographical extent of the range measurements, e.g. comprehensive *vs.* partial measures.

Range size measurements exhibit a strongly right-skewed frequency distribution with many geographically restricted species and fewer wide-spread taxa. A small number of species have idiosyncratically large ranges.

Rankings from GIS-supported, comprehensive range size assessments do not deviate much from ‘cruder’ measurements such as minimum convex polygons, latitudinal and longitudinal extents or their products.

Comprehensive ranges and partial Southeast-Asia ranges are strongly correlated, but already at this rather large partial scale the ranking of species can change considerably in comparison to global ranges. Other measures of occupancy at increasingly smaller partial scale show decreasing strength of correlations but remain highly significant.

Range area data are phylogenetically autocorrelated: Related groups of species have ranges of similar size.

Introduction

The range size of species has received considerable attention in macroecology (Maurer 1999, Holt 2003) as well as conservation biology (e.g. Thomas et al. 2000). For instance, range sizes have been associated with species' abundance (Brown 1984, Gaston 1996a, Gaston & Lawton 1988) and latitude (e.g. McPherson 2003, Chown & Gaston 2000), they are used as parameters to assess the extinction risk of species (Jones et al. 2003, Keith et al. 2000, Purvis et al. 2000, Kunin & Gaston 1997) and they are important components of theoretical models that investigate dispersal (Gaston & Blackburn 2003, Akcakaya 2000) or biodiversity and biogeography (e.g. Hubbell 2001, McGill & Collins 2003). However, conceptual problems appear once theoretically derived ideas are to be tested on empirical data: 1) Range size might be seen as a fractal (as are most environmental data, e.g. Burrough 1981, Bolliger et al. 2003), so its measurement depends heavily on the scale of measurement. Macroecological studies on the range-abundance relation, for instance, often use very different scales of range measurement, such as *occupancies* of grid cells (or less systematic entities, such as sample sites) of various size or the complete *range area* within the most extreme records of the species (the 'extent of occurrence', Gaston 2003). A general distinction was also drawn between the *comprehensive* (i.e. global) range and the *partial* range (Gaston 1996a), which describes any part of the range that is under investigation, e.g. the region where a particular field study was conducted. Studies which employ largely different scales in the measurement of range size might actually investigate different phenomena and mechanisms (Blackburn & Gaston 1998, Gaston 1996a, see also Hartley 1998) and might create artefact results at small scales under certain circumstances (Stoffels et al. 2003, Maurer 1999). 2) Except for very few taxa (e.g. birds) in Western Europe and North America, range sizes cannot be measured directly, but have to be estimated from more or less scattered data. For invertebrates, moreover those from tropical regions, data can be expected to be highly incomplete and biased with regard to sampling region, habitat and taxon (e.g. Graham et al. 2004, Fagan & Kareiva 1997, Soberón et al. 2000). Rough measurements such as latitudinal and longitudinal extent of the most extreme records, or minimum convex polygons have been used as surrogates for range size (e.g. Gaston 1994a, 2003), while for increasing precision of a range assessment assumptions about a species' habitat preference have to be made. Techniques to implement such assumptions, such as GIS-based models, are discussed in chapter 1.3 & 4.1.

Quinn et al. (1996) addressed these problems and showed in a partial range analysis of British butterflies that several range measures, from the occupancy of 100 km^2 grid cells to European ranges as well as latitudinal and longitudinal extents, correlate relatively good with each other. Similarly, Blackburn et al. (2004) found that several GIS-based, spatially detailed range estimates for the world's parrots did not yield substantially different range rankings than crude measures such as latitudinal extents. Brändle et al. (2002a) also report highly significant correlations of range measurements across different scales for European butterflies. However, Brändle et al. (2002a) as well as Cowley et al. (2001) found an influence of scale on the importance of factors that explain range size in correlation analyses (such as density, body size, dietary niche, etc.).

In this study, global distribution maps for all Sphingidae that occur in Southeast-Asia were available from a GIS-supported estimate (see below, Beck & Kitching 2004). Range sizes according to these maps are compared to 'cruder' measurements of range size, such as the area of a minimum convex polygon of records and the latitudinal and longitudinal extent. The *comprehensive* vs. *partial* range concept is explored by comparing global range estimates with partial range measures of different extent. Furthermore, range sizes are tested for phylogenetic autocorrelation and differences between sub-taxa. This explores the idea that the area that a species occupies might be connected to inherited traits of the species and thus should be more similar among closer related species.

Methods

The location of species records was mostly available at a precision of 1° latitude/longitude (Beck & Kitching 2004, see also chapter 4.1), which is equivalent to ca. ±80 km at locations near the equator. From these records, distribution maps were estimated based on habitat parameters such as vegetation zone, temperature of the coolest month, precipitation and altitudinal zone. The procedure (termed the GIS-model hereafter) is described and discussed in detail in chapter 4.1, the maps and further information on the estimation process can be found in Beck & Kitching (2004). Range areas from the GIS-model were calculated for complete maps as well as for those sections of ranges that are within Southeast-Asia (defined in this study as the region from Burma/Myanmar throughout the Malesian archipelago to the Solomon Islands, see chapter 1, Beck & Kitching 2004). Additionally, areas for minimum convex polygons (MCPs, excluding sea areas), latitudinal and longitudinal extents (both in degree) and the product of latitudinal and longitudinal extents were calculated. Additional partial range measures are the number of islands within Malesia on which a species is recorded or expected (from checklists in Beck & Kitching 2004, estimates are based on the GIS-model), and the number of local sampling sites in Borneo where a species was found (from a total of 106, see appendix I for details on most sampling sites). The latter measure must *a priori* be considered as highly biased and insufficient as a measure of range or occupancy as will be discussed below, but nevertheless even smaller-scaled measures can be found in the literature (e.g. Krüger & McGavin 2000, Pantoja et al. 1995). Not for all species records were available to calculate some of these measures (e.g., less than three recorded locations do not allow measuring a MCP), hence the reduced sample size in some of the comparisons. Area calculations were carried out with *Animal Movement Program* (Hooge et al. 1999), an extension to *ArcView 3.2* (2000), using a sinusoidial equal-area projection of the range maps.

To test for phylogenetic autocorrelation in range area data (e.g. Webb et al. 2002), the randomisation method of Abouheif (1999) was used. The *Test for Serial Independence* (Reefe & Abouheif 2003, see also Abouheif 1999) was applied to investigate the assumption of phylogenetic independence. An updated version of the systematics in Kitching & Cadiou (2000, I.J. Kitching, pers. com.) was used as a phylogeny for Sphingidae, allowing for unresolved nodes where applicable. From 3000 randomisations of the original phylogeny (flipping of the nodes, which leaves the original structure intact yet changes neighbouring relationships of values), a mean 'observed value' of the *C-statistic* (derived from summed differences between successive values ordered by phylogeny; see Abouheif 1999 for details) was calculated, which is compared to the *C-statistic* of data from 3000 randomised phylogenies. Computations were executed with the program *Phylogenetic Independence 2.0* (Reefe & Abouheif 2003). All other statistical tests were computed with the program *Statistica 5.01* (StatSoft 2003).

Results

Frequency distribution of range size measures

GIS-derived range areas for 380 hawkmoth species span five orders of magnitude, from 2,4 x 10^3 km^2 to 3,0 x 10^7 km^2, the median of the highly skewed distribution (see below) is 1,02 x 10^6 km^2. The most restricted species, *Ambulyx suluensis*, lives only on a few small islands, while the most widespread species, the Convolvulus Hawkmoth (*Agrius convolvuli*), is found almost everywhere in the old world tropics (see also maps in Beck & Kitching 2004). The frequency distributions of different range measurements for global as well as for partial ranges are strongly right-skewed (see e.g. Gaston 1998 for terminology), whereas they are left-skewed on a log-transformed axis (figure 4.11, 4.12): A large majority of species has relatively small ranges, globally as well as in relation to the species' Southeast-Asia ranges. Data of range measures are neither *normal* nor *lognormal* distributed (KS-tests, $p<0{,}01$), but all measures except longitudinal extent can be reasonable fitted to a *gamma*-distribution model (KS-test: $d<0{,}053$, $p>0{,}10$). A plot of global range sizes from the GIS-model (not shown) shows that only the presence of some very wide-ranging species deviates from this distribution model. This is further displayed in a rank-range area plot (figure 4.13), which

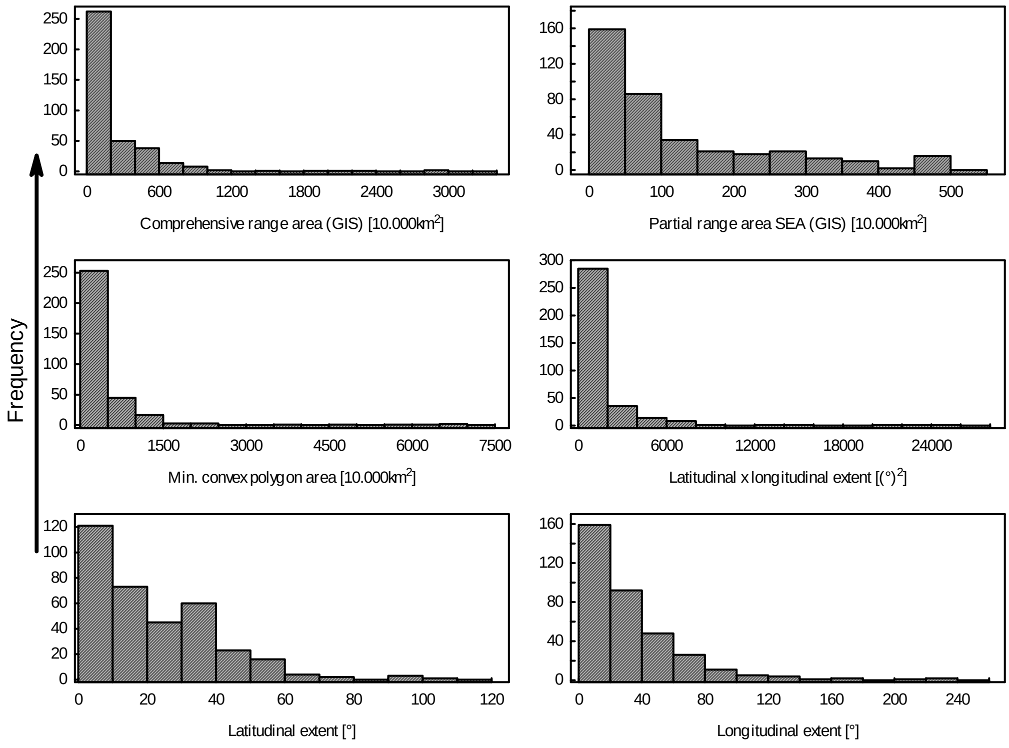


Figure 4.11 displays the frequency distribution of several range-size measures for global ranges and partial ranges (Southeast-Asia, only GIS-model: upper left graph) for 380 species of Sphingidae.

clearly shows the idiosyncratic peak of the few extremely far-ranging species. Most of these are additionally expanding their ranges by migration during favourable seasons.

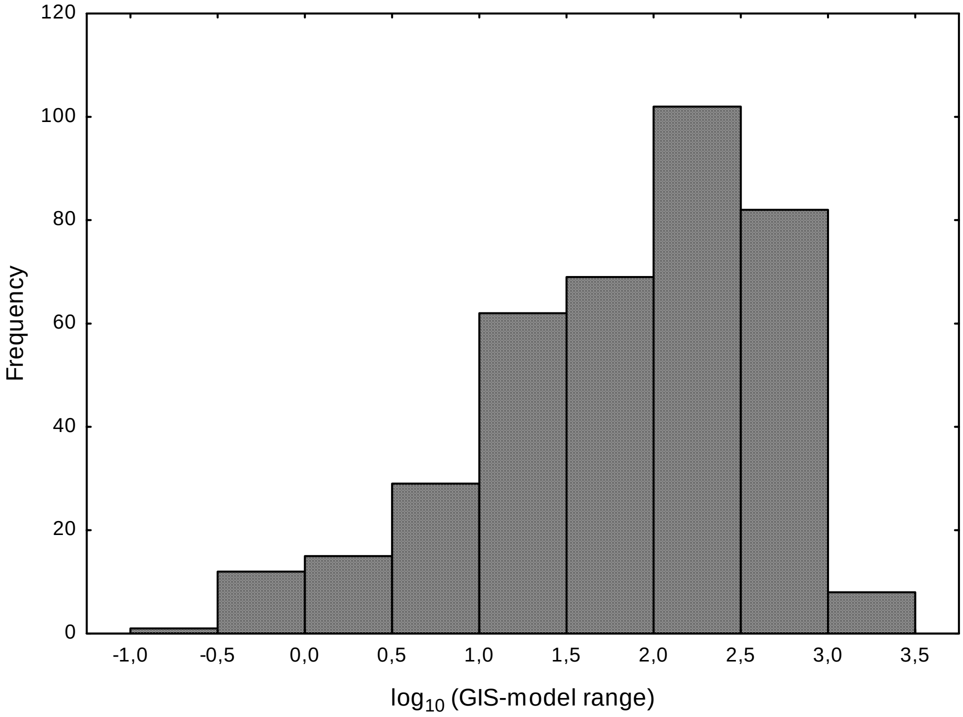


Figure 4.12 shows the frequency distribution of comprehensive range measurements from the GIS-model (same data as in figure 4.11) on a logarithmic scale.

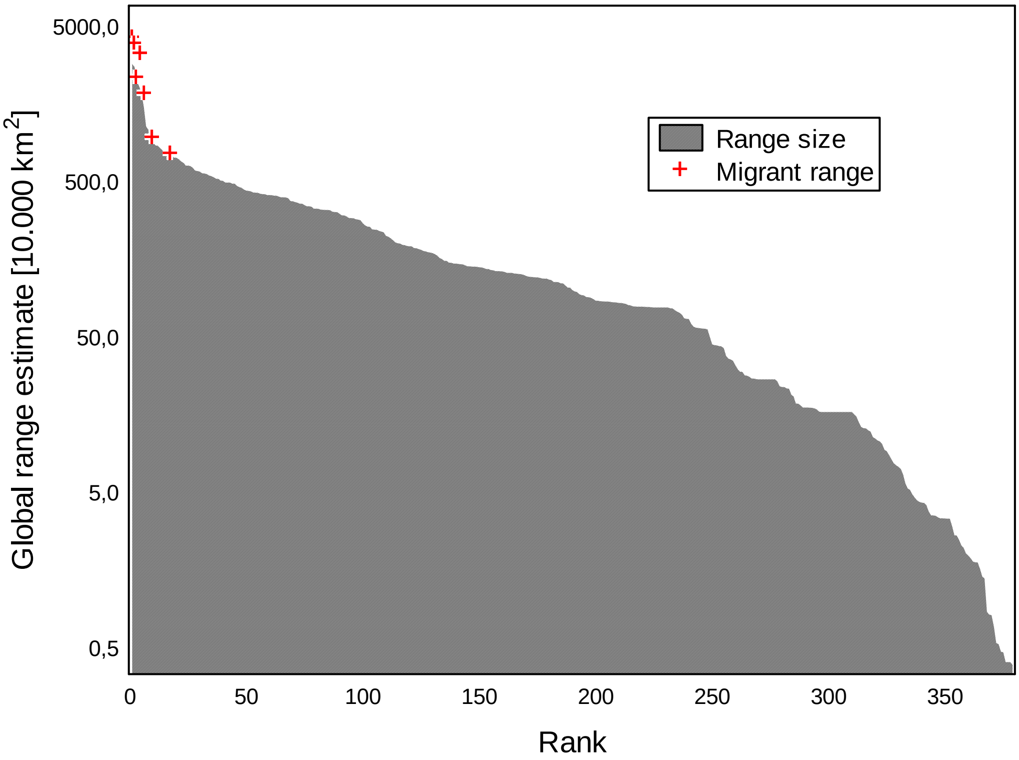


Figure 4.13 shows the distribution of comprehensive range areas for 380 species of Southeast-Asian Sphingidae (data sorted by rank).

Relative measures of range size

All measurements for comprehensive range size that were employed in this study correlate very well with each other (table 4.11). Furthermore, the correlation between the GIS-model-derived range measures and its two best ‘substitutes’ (MCP and lat. x long.) can be well described by a linear regression on a double-logarithmic plot (figure 4.14). Log$_{10}$(MCP’s), which also measure range area in square kilometres, is related to log$_{10}$(GIS-model) area sizes at a slope of 1,36.

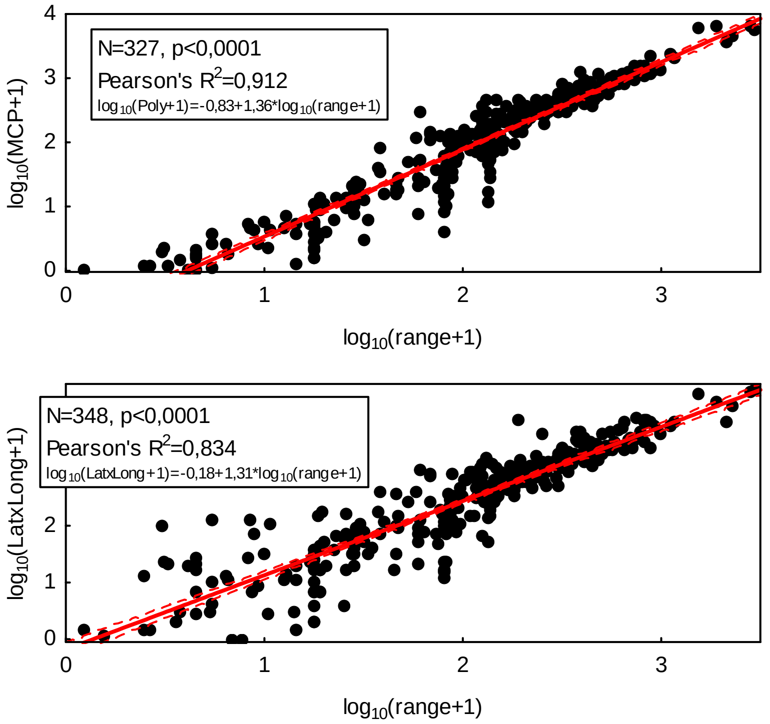


Figure 4.14 shows correlations between GIS-modelled global range estimates and two more ‘objective’ range measures, minimum convex polygons (MCP: upper figure, only land area) and latitudinal [°] x longitudinal [°] extent (lower figure).

	GIS-mod.	MCP	Lat.	Long.
MCP	0,926			
Lat.	0,847	0,853		
Long.	0,865	0,892	0,820	
Lat. x Long.	0,901	0,935	0,944	0,955

Table 4.11 shows R^2-values for Spearman rank correlations between several measures for the comprehensive ranges of Sphingidae species. All correlations are significant at p<0,0001. The number of species in pair-wise comparisons varies between 327 and 351, depending on the availability of measures (see methods).

Comprehensive *vs.* partial range

Measures of comprehensive (global) range and partial (Southeast-Asia-wide) range correlate well with each other (figure 4.15), but are not very well described by a linear relationship on a double-logarithmic scale. The plot with linearly scaled axes identifies two sets of largely deviating species: Species in the upper left area of the graph are widespread in Southeast-Asia, but are also very widespread in other parts of the old-world tropics (e.g. *Hippotion celerio*, *Agrius convolvuli*). Species in the lower left region of the graph are widespread in their global distribution, but penetrate only marginally into Southeast-Asia. Examples are temperate species such as *Hyles livornica* or *Deilephila elpenor*. The relatively low number of such species shows that the study region, Southeast-Asia, is a quite well-defined unit with respect to its hawkmoth fauna.

To further explore effects of scale, some smaller-scaled measurements of partial geographic range were taken: The sum of islands where a species is present, and the sum of local samples on Borneo. R^2-values of rank correlations between these measures are clearly getting weaker with increasing distance of scale (from global range to presence-patterns on one large island, see table 4.12), but all correlations are significant at p<0,001.

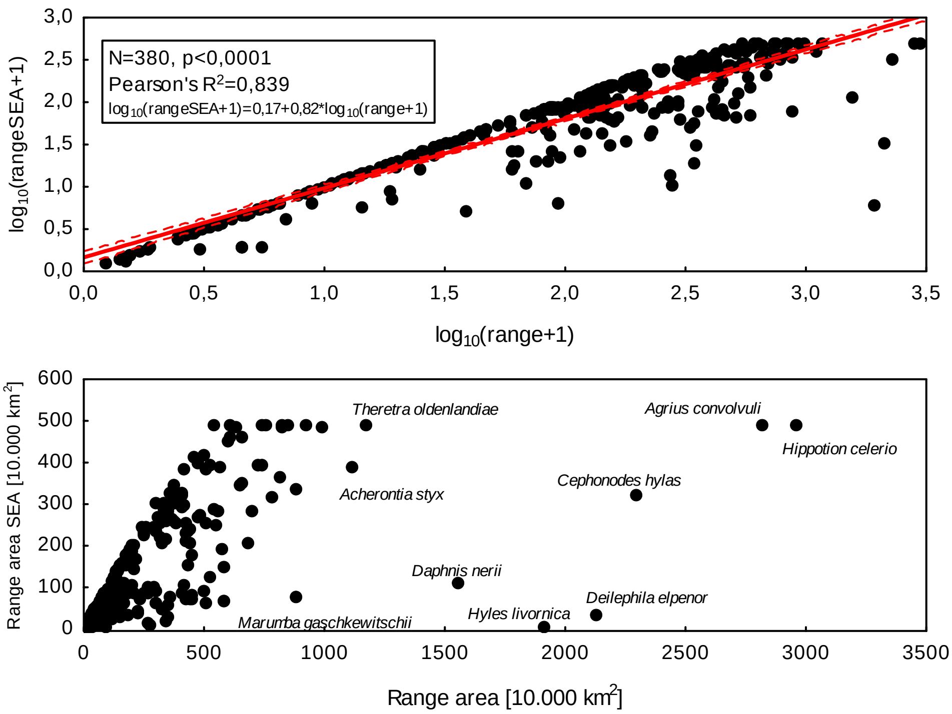


Figure 4.15 shows the relation between global range estimates and 'partial' Southeast-Asia-wide estimates (see text for details). The upper figure plots the relationship on a double-logarithmic scale, the lower figure has linear axes.

	GIS	GIS-SEA	Islands (rec.)	Islands (est.)
GIS-SEA	0,789			
Islands (rec.)	0,342	0,449		
Islands (est.)	0,253	0,353	0,900	
Sites (Borneo)	0,162	0,211	0,192	0,157

Table 4.12 shows R^2-values for Spearman rank correlations between several measures of 'range' or occupancy at different scales (see text for details). All correlations are significant at p<0,001. Sample sizes differ due to data availability: Of a total of 380 species, data on island presence (rec. & est.) were available for 306 species. Data on site presence on Borneo were available for 86 species.

Phylogenetic signal in range size

In a test for serial independence (Reefe & Abouheif 2003), only 30 of 3000 randomised phylogenies had average C-statistics which were equal or larger that mean observed C-statistic. Thus, the null hypothesis of phylogenetic independence of the range area data has to be rejected at p=0,010: Range sizes of Southeast-Asian Sphingids are positively auto-correlated due to effects of phylogeny. If only the partial Southeast-Asian range areas are used for analysis, the result is nearly the same at p=0,016 (49 of 3000 randomised C-statistics ≥mean observed).

A comparison between comprehensive range areas of taxonomic sub-groups shows no significant difference in range area between subfamilies (figure 4.16). However, already on the next lower taxonomic level of tribes, systematic differences in range area begin to show, although differences are significant only for species of the tribus Acherontiini, which have on average significantly larger ranges than other tribes.

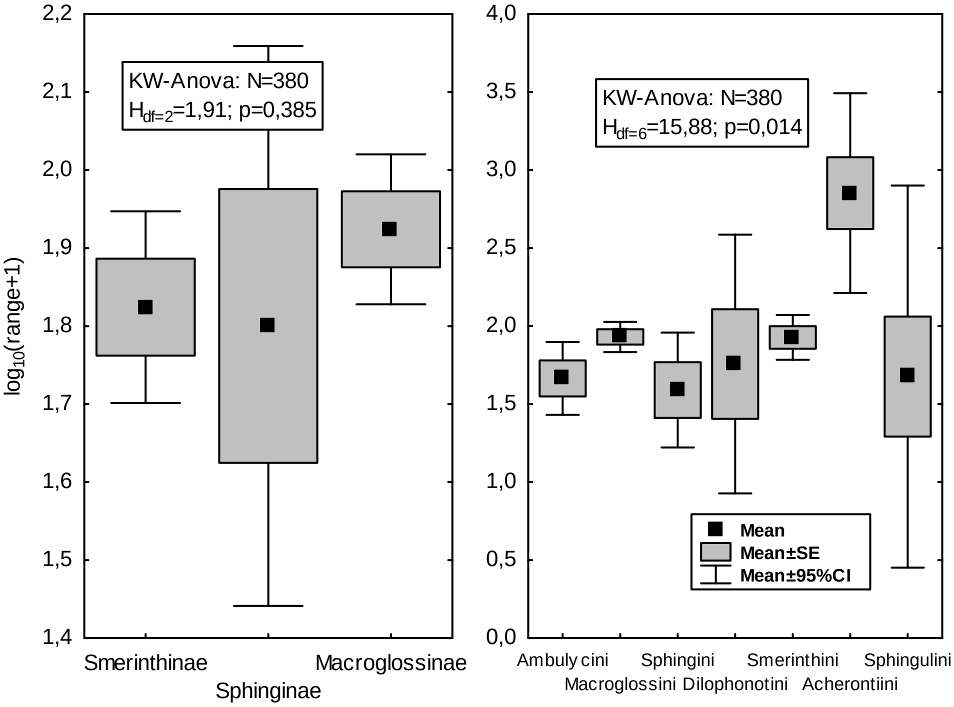


Figure 4.16 compares mean global range sizes [from GIS-model, in 10.000 km^2] between Sphingid subfamilies (left figure) and tribes (right figure). The significant difference in tribal range size is caused solely by the Acherontiini, which have significantly larger ranges than Ambulycini & Sphingini (multiple z-test, $p<0,025$).

Discussion

Frequency distributions of range sizes

Range areas exhibit a strongly right-skewed frequency distribution with many geographically restricted species and fewer wide-spread taxa. The pattern persists even if only partial Southeast-Asian ranges are used, thus eliminating the very large range classes. This is in marked contrast to the data on partial British ranges of butterflies and molluscs presented in Quinn et al. (1996), many of which showed centred or left-skewed distributions. It must be suspected that this is mainly an effect of using partial range measures in the latter study. Large-scale environmental variation (such as climate or vegetation zones), which limits the extent of species' ranges (e.g. Quinn et al. 1997, 1998), is probably considerably smaller within Britain than it is at the scale of most species' comprehensive range: Except of specialists in geographically clumped habitat types, many of the species that occur in Britain can live in most regions on the island. At a finer resolution of measurement (occupancy of 100 km^2 grid cells), Quinn et al's (1996) data approach a right-skewed distribution, which appears to be the most common form of range area frequency distributions (e.g. Gaston

1996b, Gaston & He 2002, and references therein), although variation is high across studies (Gaston 2003; note a confusion in the literature: Gaston 1998 reports a *left-skewed* distribution range sizes for Australian birds on a *log-scaled* range-axis, matching findings reported here, figure 4.12). Blackburn et al. (2004) found right-skewed distributions for comprehensive ranges of parrots that got weaker at low spatial resolutions. Additionally, the strongly prevalent biogeographical effects within the Malesian region (e.g. Holloway 1987b, chapter 4.1) could at least a partly be responsible for of the large number of geographically restricted species as the isolation of islands or archipelagos might have promoted speciation and limited the dispersal of species into other regions. While speciation and extinction can certainly influence range size distributions (e.g. Gaston & Chown 1999), processes in ecological time scales are probably also playing an important role in creating observed patterns. Gaston & He (2002) have provided an explanatory model which predicts the distribution of range sizes based on the effects of stochastic abundance fluctuations of each species, which fits to a number of data sets. No attempt was made to fit this distribution to the Sphingid data, but a frequency plot (figure 4.12, log-scaled as in Gaston & He 2002) reveals a slightly left-skewed distribution which has good graphic resemblance to those data which fitted Gaston & He's (2002) model.

A small number of species have idiosyncratically large ranges which clearly stand out from the rest of the range area distributions (see figures 4.12 & 4.13). Of the six species with ranges larger than 1,5 x 10^7 km^2, one (*Deilephila elpenor*) is of Palaearctic distribution but reaches only marginally into northern Southeast-Asia (see Beck & Kitching 2004 for distribution maps). *Daphnis nerii* is an afrotropical and western Asian species, while its Southeast-Asian and Pacific range is rather scattered. There are indications that this species is strongly expanding its range in recent times through human activities, possibly because of the modern spread of its larval hostplant *Nerium* as a garden ornament. For instance, in Borneo the species is common in the suburban area around Sandakan (Chey 2002b), but has never been caught inland, neither in natural nor in traditionally cultivated areas. *Hyles livornica* is also an afrotropical and West-Asian species which, unlike *D. nerii*, did almost not at all penetrate into Southeast-Asia. The remaining three 'extra-wide' ranging species (*A. convolvuli*, *Hippotion celerio* & *Cephonodes hylas*) are widespread in the African as well as Asian tropics. While the latter species shows morphological differences between regions that lead to the recognition of an African and a mainland Asian subspecies (as well as two restricted subspecies at the south-eastern edge of its range), the former two species appear uniform across their huge range. None of these extra-wide ranging species is from the subfamily Smerinthinae. In Southeast-Asia, Smerinthinae have, in comparison to other subfamilies, a tendency to be more abundant in primary habitats (chapter 3.1), at medium altitudes (chapter 3.1, Schulze 2000), and they show a higher species turnover across the islands of Malesia (chapter 4.1). These features were associated (chapter 3.1 & 4.1) with their deviating life-histories as *capital breeders*, while Sphinginae and Macroglossinae are adult-feeding *income breeders* (Lemaire & Minet 1998). The most wide-ranging Smerinthinae species is *Marumba gaschkewitschii* on range area rank eleven. However, seven subspecies were recognized for this species (and some more described, see Beck & Kitching 2004), an indication that populations within the species are (or were) quite isolated. A further analysis of life-history parameters of the extra-wide ranging species might give important clues about the ultimate causes for the size of a species range.

Correlations of different range size measurements

Rankings from a GIS-supported range size assessment do not deviate much from 'cruder' measurements such as MCPs or latitudinal x longitudinal extent. This confirms results from studies on British butterflies and molluscs (Quinn et al. 1996) as well as the comprehensive ranges of the world's parrots (Blackburn et al. 2004). Blackburn et al. (2004) also compared results of several macroecological correlations, based on different range measures, and concluded that the spatial resolution of range measurements did not influence general results much. Blackburn et al.'s (2004) range measures were all based on the same distribution maps, which they considered a weakness of their analysis. Results of this study confirm the result of good correlations of different range size measures with one another, based on figures that were not based on distribution maps but on the original distribution records. However, not all measures of distribution could be tested in this way: The recorded occupancy of grid cells was too strongly biased by undersampling effects (see also chapter 4.1) and was ignored as a range measurement.

The most precise measurement might not always be the best for all analyses (see also Blackburn et al 2004). For examples, the distribution of land and sea in Southeast-Asia and the Pacific is very uneven and biased on a Northwest-Southeast gradient: To occupy the same range *area*, a species needs to be much more widespread over the South Pacific islands than in mainland Asia. Thus, in some instances (e.g. for an assessment of dispersal abilities) latitudinal and longitudinal extent of species might be more appropriate measures than range area.

Comprehensive *vs.* partial range

Comprehensive ranges and partial Southeast-Asia ranges are strongly correlated, but already at this rather large partial scale the ranking of species can change considerably in comparison to global ranges. This applies particularly to two sets of species, the extremely wide-spread ones (see above), and those for which Southeast-Asia is the very edge of their global distribution. The main reason for partial range approaches in macroecology is a lack of comprehensive range data, particularly for tropical invertebrates (Maurer 1999). The sub-continental scale of partial Southeast-Asia is still far from a 'small-scaled' approach, but rank changes in a number of species become already evident (figure 4.14).

In a further comparison of 'range' measures, data on four different scales were compared: (1) the global extent of occurrence, (2) the partial restriction of this occurrence to the subcontinent Southeast-Asia, (3) the occupancy of islands in an archipelago which spans roughly 8.000 km in its widest extent (recorded data contain undersampling biases, which are supposed to be corrected in estimated data, see chapter 4.1), and (4) the occupancy of sites within Borneo, which at a size of ca. 7,35 x 10^5 km^2 is roughly 3 times the size of Britain. Thus, the extent of the latter can still be considered large enough to not sample only effects of local habitat conditions, but true range effects: Within Borneo, effects of geographic distance were shown on faunal turnover of Sphingid assemblages (chapter 3.1). The Borneo data, however, contain clear flaws in quality: local species assemblages from own sampling as well as published and unpublished sources (see chapter 3.1 & appendix I) stem neither from systematic nor from truly random sampling of grid cells. Instead, sampling sites were chosen to maximise habitat heterogeneity at the lowest possible logistic costs. However, despite all the conceptual differences between these range measures, which might actually measure quite different processes (e.g. dispersal ability on the large scales, niche breadth on the small scale), all measures are significantly correlated, though at decreasing quality with increasing differences in scale. This indicates that 'range size' is indeed a scale-related problem, which possibly extends even to 'local abundance' as the smallest possible scale of 'partial range' measurement. Until adequate null models are available which allow testing 'mechanistic' macroecological effects against 'baseline' correlations that must be expected (see also Hartley 1998), macroecological correlations at close-by scales are probably better avoided as they carry a greater chance of scale-dependent artefacts. For instance, a positive correlation between local abundance and global extent of occurrence (e.g. as area or latitudinal/longitudinal extent) requires more biological explanation than one of local abundance and local occurrence on sample sites.

Phylogenetic signal

Range area data of Southeast-Asian hawkmoths carry a phylogenetic signal: Related groups of species tend to have ranges of similar size. The same effect was found for parrot range areas (Blackburn et al. 2004). Although this is not surprising from a theoretical perspective (similar, inherited biological features can lead to similar geographical extent, Kunin & Gaston 1997, see also Jablonski 1987), but still was counterintuitive as many of the more specious Sphingid genera have both very restricted as well as very widespread species (see also Gaston 1998). This has two practical implications for further research: (1) Range sizes are not randomly distributed, but are at least partly determined by a set of inherited characters. Thus, in might be possible to identify such characters by comparative methods (see also Webb et al. 2002), e.g. by searching for synapomorphic ecological characteristics that may make Acherontiini more widespread than other Southeast-Asian Sphingidae tribes. (2) For comparative analyses between geographic range and other features of species (e.g. body size, niche breadth, local abundance), effects of phylogeny must be considered for a proper evolutionary interpretation (e.g. Garland & Ives 2000, Garland et al. 1999, Harvey & Pagel 1991), and correction methods such as independent contrast (Felsenstein 1985) should be applied to confirm that relations are effects of the variables in analysis, not of phylogeny.

CHAPTER 5 – NICHE DIMENSIONS

CHAPTER 5.1 - LARVAL HOST SPECTRUM AND DIETARY BREADTH

Abstract

Larval host plant relationships for 168 Southeast-Asian Sphingidae were analysed on the level of plant families.

Hawkmoths appear as a relatively polyphagous group, 28 percent of the caterpillar species are feeding four or more host plant families. Host plants from 112 plant families were recorded, the most commonly recorded plant families are Rubiaceae, Vitaceae and Aracea. Diet breadths of species are phylogenetically autocorrelated: Closely related species utilise a similar number of host plant families.

Average diet breadth (number of recorded host plant families) differs between Sphingidae taxa: Sphinginae, particularly the species of the tribus Acherontiini, utilise a significantly larger number of plant families than other Sphingidae groups.

Differences in the host plant family spectrum of hawkmoth species were analysed with non-metric multidimensional scaling (MDS), which revealed a) that Smerinthinae species, as well as the Sphinginae-tribus Sphingini, use a tight group of host plants which are nested in the host plant spectrum of Macroglossinae (rather than non-overlapping, as has been suggested in earlier literature), and b) that some members of the Sphinginae-tribus Acherontiini stand out from the 'usual' host plant spectrum of hawkmoths by using more host taxa and, at least in one species (*Acherontia lachesis*), also different plant families than other Sphingidae.

The diversity of utilised host plants among Sphingidae families (measured as Fisher's α of host plant families) was found to be significantly lower in Smerinthinae than in other subfamilies, confirming the above mentioned results.

Potential biases of data due to incomplete host records are discussed and must be considered, results should be treated as tentative.

Introduction

The host plant relationships of tropical herbivorous insects are a much discussed topic in community ecology (e.g. Novotny et al. 2004, Novotny et al. 2002a, b, c, Fiedler 1998). They are important parameters in the estimation of global biodiversity (Ødegaard et al. 2000) and are a central issue in the discussion on niche breadth and the role of competition in the structuring of communities (see Denno et al. 1995, Hartley & Jones 2003, Strong et al. 1984). Diet breadth is probably an essential niche dimension for herbivorous insects (e.g. Novotny et al. 2002b) and has been used to explore the influence of niche breadth on macroecological variables such as body size (Loder et al. 1998), range size or abundance (see e.g. Gaston et al. 1997). The distribution of host plants can restrict the distribution of an herbivore, but is not the only factor that is limiting an herbivore's range size (Quinn et al. 1997a, Lawton 2000) or its local abundance (e.g. Gaston et al. 2004).

Many herbivore insects appear relatively specifically bound to one or a few genera of plants (e.g. Ward & Spalding 1993), although recent literature suggests higher diet breadths than previously assumed for tropical regions (Novotny et al. 2002c, Ødegaard et al. 2000, Fiedler 1998). Restrictions in diet might be an adaptation to plant chemistry, the result of selection by predators and parasites (e.g. Jaenike 1990, Coley & Barone 1996, Dyer 1995, Bernays & Graham 1988 and references therein), a result of positive feedback processes in evolution (Crespi 2004 and references therein) or a means to avoid poisonous plants in the face of limited discrimination abilities (Nylin et al. 2000, Janz 2003, Bernays 1998). A broad spectrum of host plants leads to more available resources, both locally as well as regionally. Thoroughly studied systems of Heliconiid butterflies in South- and Central America (Gilbert & Smiley 1978) showed that complex interactions of predator avoidance, stratification, cannibalism and mimicry can shape host plant choice and structure the community (see also Lill et al. 2002, Stireman & Singer 2003, Barbosa & Caldas 2004, Scheirs & DeBruyn 2002).

Caterpillar communities of Bombicoidea were studied in great detail by Janzen (1981, 1984, 1988) in a neotropical dry forest in Costa Rica, who characterised them as relatively host-specific folivores under local conditions. Furthermore, he noticed that the dichotomy in life history between neotropical Sphingidae (feeding adults, iteroparous, long-lived, 'intelligent' adults) and Saturniidae (non-feeding adults, semelparous, short-lived adults; see Janzen 1984) also extends to the larval feeding patterns of these groups: Apparently neotropical Sphingidae typically feed on young leaves of plants, which contain small toxic molecules that can be detoxified by specialised enzymes, whereas Saturniidae feed in tough leaves of plants with high contents of tannins or other molecules that make digestion difficult (Janzen 1981, 1984). Allometries of mandibles and observations of gut contents seem to confirm these different forms of phytophagy (Bernays & Janzen 1988). As a result, Sphingidae caterpillars eat much more nutrients 'per bite' and need less time to reach pupating size (Bernays & Janzen 1988). This situation cannot be directly transferred to the oriental and Australasian region, where Saturniidae are much less specious (and represented only by one subfamily, the Saturniinae), while the Sphingid subfamily Smerinthinae is rich in species in Asia (Holloway et al. 2001), but not important in the neotropics. Holloway (1987a) suggested that in Southeast-Asia much of Janzen's (1984) dichotomy among the 'tropical big moths' is found between the Sphingid subfamilies Smerinthinae (with a Saturniid-life style, but see chapter 1.2: adults of the tribus

Ambulycini are flower feeding) and the Macroglossinae & Sphinginae (with a 'Sphingid' life style; see also chapter 3.1, box 3.1). Holloway (1987a) noted that the inventory of larval host plant families does not overlap much between these two groups of Sphingidae on Borneo.

Two approaches have been used to acquire host plant data for studies on the diet breadth of local or regional assemblages: Feeding trials of sampled insects in local field studies allow comparing the food spectrum and host specialisation at a site (e.g. Novotny et al. 2004, 2002a, b, Barone 1998, see also Janzen & Hallwachs 2004), but need to be extensive in order to yield data which are not hopelessly biased by undersampling (see e.g. Basset et al. 2004). Alternatively, host plant records can be compiled from published data, which is particularly an option for some Lepidoptera taxa (e.g. many butterfly groups) that can be reliably identified for cross-referencing between studies and that have been sampled and raised by enthusiasts for more than 150 years, albeit in different parts of a species' range. For instance, Fiedler (1998) has used such data to compare the diet breadth of European and Southeast-Asian butterflies. However, even very well sampled tropical taxa must still be suspected to be influenced by undersampling to an unknown degree (see also discussion), no matter which of the two approaches is employed. Magnitude and direction of such biases are difficult to assess as two antagonistic effects contribute to them: Rarely encountered species have few host plant records just because they have not been found often enough. Records for very common species, on the other hand, might not be reported as they are 'nothing special', particularly if they refer to plant taxa that have been recorded already.

In this analysis, the following topics of larval host plant use of Southeast-Asian Sphingidae are explored:

1) Are there systematic differences in the diet breadth between taxonomic sub-groups of the hawkmoths? In this context, is the diet breadth of Sphingidae related to their phylogeny as has been suggested for other taxa (e.g. Holloway & Hebert 1979 for tropical moths, see also Brändle et al. 2002b for European birds)?

2) Is there a division of the utilised host plant spectrum between taxonomic sub-groups of the hawkmoths?

3) Is there a difference in the diversity of utilised host plants among taxonomic sub-groups of the hawkmoths?

4) To what extent do host plant ranges have the potential to limit the ranges of Sphingidae species?

Methods

The host plant data bank

A data bank of the larval host plant records for Southeast-Asian hawkmoths was available for analysis through the generosity of Dr. Ian J. Kitching of the Natural History Museum (London). 3.175 host plant records were compiled from published literature as well as unpublished sources and contain the data in Robinson et al. (2001a) or its corresponding internet site (Robinson et al. 2001b), as well as some recent additions and updates.

For the purposes of this analysis, Sphingidae species (nomenclature as in Kitching & Cadiou 2000 and some recent new descriptions, see e.g. Beck & Kitching 2004) were the lowest taxonomic level of analysis, while subspecies data were mostly ignored. Plant data were usually available at least for genera, but were not analysed on a more detailed taxonomic level than families. Plant families were often shown as the taxonomically relevant level of host plant specialisation in Lepidoptera (Ward & Spalding 1993, Fiedler 1998, Ackery 1991, but see Novotny et al. 2002c, who suggest plant genera specialisation). Furthermore, the use of higher taxonomic units in the analysis of plant data lowers the risk of artefacts from undersampling. Plant classification follows the angiosperm systematics of APG (1998), not traditional plant families and orders. The APG-system is based on molecular supertrees and reflects Lepidopteran food choice better than older systems (I.J. Kitching pers. com.). Families and in some cases 'higher taxon orders' (HTOs, the equivalent of classical plant orders) were used for Sphingid host plant analysis.

The Sphingid species *Hippotion boerhaviae* and *H. rosetta* pose potential problems as they were easily confused (see Beck & Kitching 2004 for pictures), particularly in older sources. Therefore, a number of the older *boerhaviae* records might actually refer to *rosetta*. Data for these taxa were excluded from analysis. A similar problem occurs in the genus *Psilogramma*, where several subspecies were elevated to species rank in recent years (Kitching & Cadiou 2000). Data were retained in this group as subspecies information was often available which allowed determining the species according to modern classification. These cases highlight the problems of using multi-source data with multiple error possibilities (i.e., misidentification of insect or plant, erroneous interpretation of field observations, acceptance of unnatural food under experimental conditions), but emergent patterns from large databases should be robust against a small proportion of unreliable records (see discussion in Fiedler 1998 and references therein). After exclusion of the above mentioned species as well as undetermined plant family data, 3.151 records remained for analysis.

Measuring the degree of polyphagy and host plant diversity

The dietary niche breadth of species was measured as the number of recorded host plant families (see above) and HTOs. Additionally, species were sorted in a system of monophagous (only one plant family utilised), oligophagous (2-3 families utilised) and polyphagous species (≥4 plant families utilised), following the classification of Fiedler (1998). To analyse the degree of polyphagy among higher taxonomic units (subfamilies, tribes), the frequencies of species in those classes were compared in χ^2-tests (calculated with the software *StatXact 4.0*, Cytel 1998). Furthermore, Fisher's α (±95 percent confidence intervals) were calculated as a measure of host plant diversity (see e.g. Fiedler 1998 for methods) from the number of records and the number of utilised host plant families for subfamilies and tribes, using the software *Programs for Ecological Methodology* (Kenney & Krebs 1998).

Phylogenetic independence

To test for phylogenetic effect on the dietary niche of species (i.e., do related species use a similar number of host plant families?) the randomisation method of Abouheif (1999) was used. The *Test for Serial Independence* (Reefe & Abouheif 2003) was applied to investigate the assumption of phylogenetic independence. An updated version of the systematics in Kitching & Cadiou (2000, I.J. Kitching, pers. com.) was used as a phylogeny for Sphingidae, allowing for unresolved nodes where applicable. From 3000 randomisations of the original phylogeny (flipping of the nodes, which leaves the original structure intact yet changes neighbouring relationships of values), a mean 'observed value' of the *C-statistic* (derived from summed differences between successive values ordered by phylogeny; see Abouheif 1999 for details) was calculated, which is compared to the *C-statistic* of data from 3000 randomised phylogenies. Computations were executed with the program *Phylogenetic Independence 2.0* (Reefe & Abouheif 2003).

Analysing similarity in host plant use: Multidimensional Scaling

Multidimensional scaling (MDS) is a powerful tool to ordinate ecological data (which often do not follow standard statistical distributions) by similarity indices or other measures of distance (e.g. Legendre & Legendre 1998). While it has frequently been employed in biodiversity studies in recent years (e.g. Beck et al. 2002, Brehm & Fiedler 2004, see also chapter 3.1) to display the relation of faunas on different sites, it has been rarely used to analyse host plant relationships of species (but see Holloway & Jardine 1968). Here, MDS is used to display the similarity of Sphingidae species according to their host plant spectrum. Data for recorded host plant families for each hawkmoth species were used for MDS (see Cox & Cox 1994 for procedure), using Euclidean distance measures.

The Bonferroni-correction of error probabilities according to Hochberg (1988) was applied to control for spurious results due to multiple tests from the same data set.

Results

Host plant data for 168 Sphingid species (44,2 percent of 380 species in the region, see Beck & Kitching 2004) were available for analysis. Host plants from 112 plant families were recorded, the most commonly recorded plant families were Rubiaceae (55 hawkmoth species

a)	Macroglossinae	Smerinthinae	Sphinginae
monophagous	56 *(51%)*	22 *(51%)*	4 *(24%)*
oligophagous	30 *(28%)*	14 *(33%)*	5 *(29%)*
polyphagous	23 *(21%)*	7 *(16%)*	8 *(47%)*

b)	Macroglossini	Dilophonotini	Ambulycini	Smerinthini	Sphingulini	Acherontiini	Sphingini
monophagous	56 *(52%)*	0 *(0%)*	3 *(25%)*	18 *(60%)*	1 *(100%)*	1 *(25%)*	3 *(23%)*
oligophagous	29 *(27%)*	1 *(50%)*	5 *(42%)*	9 *(30%)*	0 *(0%)*	0 *(0%)*	5 *(39%)*
polyphagous	22 *(21%)*	1 *(50%)*	4 *(33%)*	3 *(10%)*	0 *(0%)*	3 *(75%)*	5 *(39%)*

Table 5.1 shows the number of monophagous (one utilised host plant family), oligophagous (2-3 host plant families) and polyphagous (≥4 host plant families) species for Sphingid (*a*) subfamilies and (*b*) tribes. See text for significance tests of frequency differences.

feeding), Vitaceae (41 hawkmoth species) and Aracea (30 hawkmoth species).

Diet breadth

Recorded host plant families range from one to 33 for Southeast-Asian species. Sphingidae are a relatively polyphagous group, a median of five host plant families per Sphingid species was found (lower, upper quartile: 2, 13, N=51; only species ≥12 host plant records were used for this calculation to minimise undersampling effects). Only nine species (17,6 percent) in this group are specific to one plant family.

In table 5.1 frequencies of monophagous, oligophagous and polyphagous species in each Sphingid subfamily and tribe are shown. Despite strong trends towards more polyphagous species among the Sphinginae, differences between subfamilies are not significant (3x3 table, $\chi^2_{df=4}=8{,}099$, p=0,087), while differences between tribes are very close to statistical significance (3x7 table, $\chi^2_{df=12}=19{,}34$, $p_{MC}=0{,}056$; exact p-value from Monte Carlo simulation (10.000 runs) were used due to many zero-values in data).

Figure 5.1 compares the mean number of host plant families per species, on HTO and plant family level, for Sphingidae subfamilies and tribes. Sphinginae use significantly more plant families than other subfamilies, and this is mainly caused by the high level of polyphagy in the tribus Acherontiini. The same patterns are repeated on the level of HTO, albeit without statistical significance, which suggests that patterns are not merely artefacts of undersampling biases.

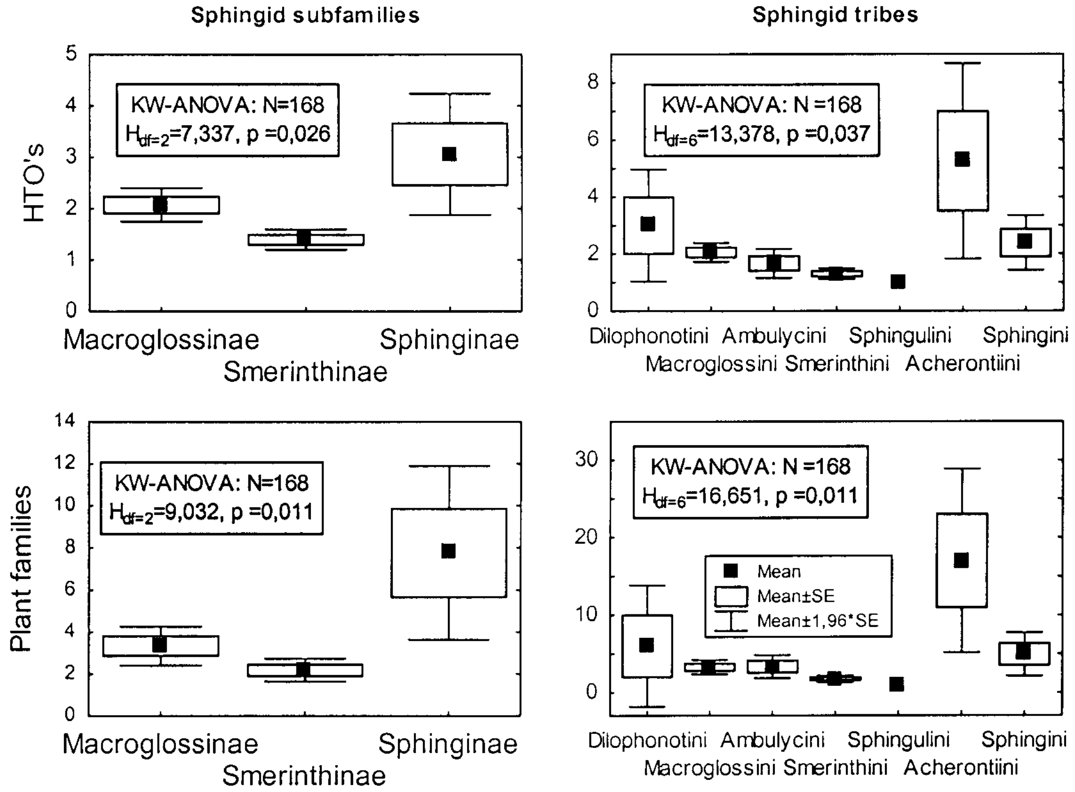


Figure 5.1 shows comparisons of mean utilised plant taxa per species. Multiple pair-wise comparisons (z-tests, two-sided) within the non-parametric ANOVA indicate significant differences between Sphinginae and the other two subfamilies for the analysis on plant family level (p<0,03), but not for HTO-data. Multiple pairwise comparisons do not yield significant results for Sphingid tribes. An appliance of the Bonferroni-correction according to Hochberg (1988) makes the subfamily-comparison for HTOs non-significant.

Phylogenetic signal

The *Test for Serial Independence* (Reefe & Abouheif 2003) was used to analyse the number of recorded host plant families for phylogenetic autocorrelation (Abouheif 1999). Only one of 3000 simulated C-statistics was equal or larger than those of the real data set. Thus, the null hypothesis of phylogenetic independence is rejected at an error probability of p=0,0003. Closely related taxa use a more similar number of plant families than less related taxa (note that this test does not refer to the identity of plant taxa).

To account for the possibility of subfamily-specific undersampling (see discussion), the two larger subfamilies were also tested separately for phylogenetic independence (but these tests were not included into Hochberg's (1988) correction of error probabilities, as they did not constitute an own result; see also Moran 2003). Diet breadths are phylogenetically non-independent for Smerinthinae (p=0,042) as well as Macroglossinae (p=0,004), thus confirming results for the whole family Sphingidae.

Differences in host plant use

The dietary segregation on plant family level that Holloway (1987a) reports between the Macroglossinae, Smerinthini and Sphingini of Borneo (referring to similar findings of Janzen 1984 in Costa Rica) is not evident for Southeast-Asian data. Between the tribes Macroglossini, Smerinthini and Sphingini, seven plant families are shared, while an additional inclusion of the Ambulycini still leaves three shared host plant families.

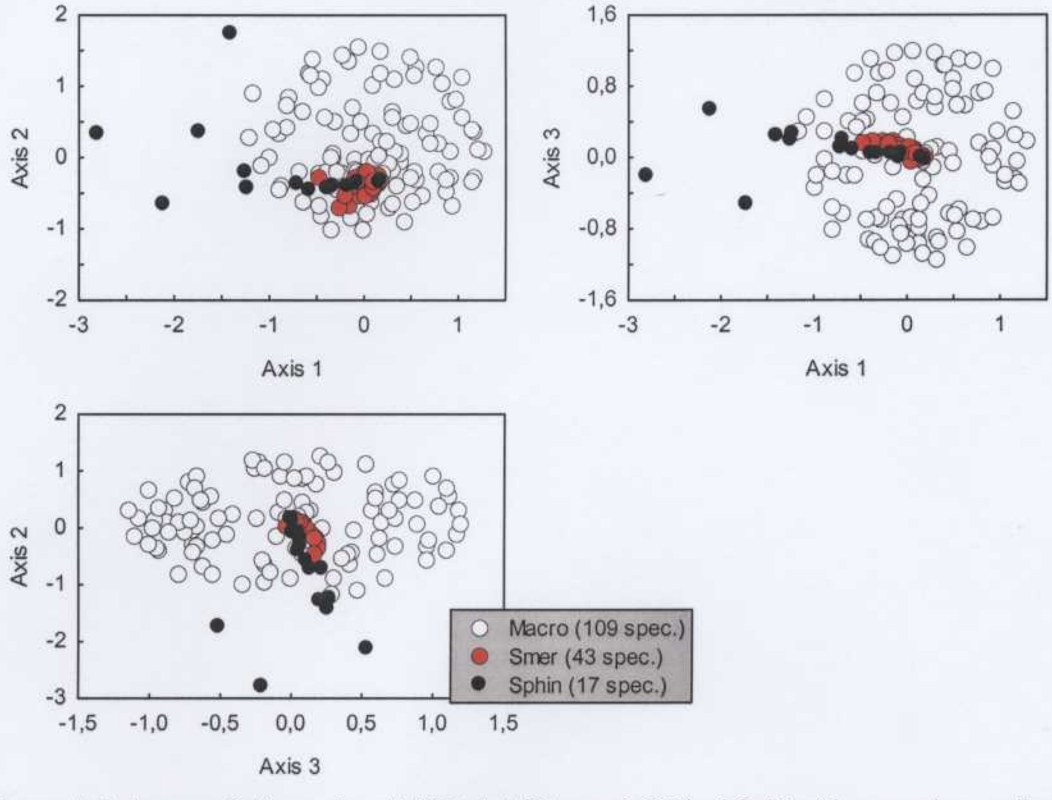


Figure 5.2 shows a 3-dimensional MDS-plot (Stress=0,320) of Sphingidae species, ordinated by larval host plant family use. Subfamily affiliation of the taxa is indicated by colours.

The large amount of data makes a tabular display (as in Holloway 1987a) not feasible. Instead, a non-metric MDS-plot is used to display similarities and overlap in host plant family use (figure 5.2). The most obvious result of this ordination is an apparently nested host plant spectrum of the Smerinthinae within the far more scattered spectrum of the Macroglossinae. Rather than being separated from the other subfamilies, Smerinthinae seem to use only a small subset of the other subfamilies' host plant families. However, Smerinthinae still use 12 plant families exclusively, which might be hidden in the graphs due to the relative high information loss in the 3-dimensional MDS (high stress value, see figure 5.2).

The Sphinginae follow a similarly nested pattern within the food plant relationships of Macroglossinae, but some species clearly stand out from this pattern and seem to use a very different food spectrum than other Southeast-Asian Sphingidae. The three most outstanding species are the Convolvulus Hawkmoth (*Agrius convolvuli*, tribus Sphingini) and the two Death's Head Hawkmoths (*Acherontia lachesis* & *A. styx*, tribus Acherintiini). In two cases their idiosyncrasy is the large number of utilised plant families rather than the exclusive use of plant taxa (*A. convolvuli*: 23 families/2 exclusively utilised families; *A. styx*: 15 families/0 exclusively utilised families), while *A. lachesis* additionally uses a number of unusual families which are not taken by any other Sphingid species in Southeast Asia (29 families/7 exclusively utilised families, e.g. Cannabaceae, Zingerberaceae, Agavaceae, Acanthaceae).

A display of the MDS results on tribus level (not shown) did not yield any further insights.

Diversity of host plant use

Figure 5.3 shows Fisher's α as a measure of host plant diversity for the three Sphingid subfamilies. As evident already from figure 5.2, the diversity of utilised host plant families of Smerinthinae is much lower than that for Macroglossinae or Sphinginae. An analysis of the diversity of host plants among the larger tribes (not shown) does not show any further differentiation within the subfamilies.

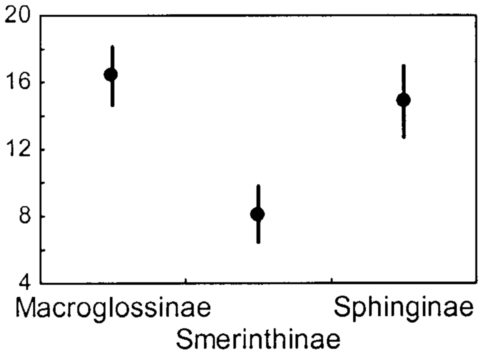


Figure 5.3 shows Fisher's α (± 95% confidence intervals) as a measure of diversity of utilised host plant families among Sphingidae subfamilies.

Host plant distribution and their implication on Sphingid ranges

The geographical distribution of Sphingid moths might be determined to a certain extent by the distribution of their host plants. Moth distribution maps were available through a GIS-supported range estimate (Beck & Kitching 2004, see also chapters 1.3 & 4.1), which does not explicitly consider host plant distribution except by utilising maps of large-scale vegetation zones. Therefore, they provide more or less 'independent' data for moth and plant distributions. The geographical distribution of host plant families for 98 of 112 recorded larval host plant families of hawkmoths could be found in various literature sources (van Steenis & Holttum 1959-2002, Keng 1969, Keng et al. 1998, Ridley 1967, Argent et al. 1999). The descriptions of each family's geographical range were grouped into four classes, the frequencies of which are presented in table 5.2: More than two thirds of the host plant families are either globally distributed (at least in the old world, which is where Southeast-Asian Sphingidae species are found) or of pantropical range. The former is of not much concern when looking for host plant ranges which potentially limit moth distribution. The same applies to plant families of pantropical distribution if one acknowledges that the northern limit of a moth species, or the southern limit in the southern hemisphere, is likely to be determined directly by climate instead of a limitation *via* food plant availability (see e.g. Quinn et al. 1997, 1998).

For these reasons, only the remaining distribution classes were scanned for cases of common distribution limits of host plants and moths, i.e. plant families of mainly temperate (Northern or Southern) distribution, which do not occur in the tropics or are confined to montane and alpine regions and plant families that had some other, idiosyncratic distribution limits in the Indo-Australian region. For these plant families it was systematically examined 1) what species of hawkmoth is feeding on it, 2) if the limit of any of the hawkmoth species or at least one of its geographical limits is congruent with that of the plant family, and 3) if the hawkmoth species does not feed on any other plant family that transgresses these limits.

Distribution class	Plant family	%
Worldwide*	27	*30,0*
Pantropical/subtropical*	41	*44,6*
Temperate (if in the tropics, mostly montane)	9	*9,8*
Restricted range	15	*16,3*

Table 5.2 lists the frequency of distribution classes for 92 of 112 recorded larval host plant families. See text for method of classification and data sources. *) occasionally refers to families which are not present in the new world.

No such case was found among the distribution class of mainly temperate or tropical-montane plant families. Most hawkmoth species were either considerably more tropical in their distribution than the respective food plant (because they fed also on other plants; e.g. *Acherontia styx*, see Beck & Kitching 2004 for distribution maps) or they also fed on other food plants with a tropical distribution, so their temperate range was not due to food limitation in tropical areas (e.g. *Deilephila elpenor*, which feeds on many temperate families, but is also frequently recorded on plant families of tropical distribution such as Araceae, Balsamicaceae). The closest case to a potential distribution limit due to food plant availability is the genus *Sphinx* (2 species), which feeds exclusively on Pinaceae. Pinaceae do not commonly occur in most lowland regions in tropical Asia and *Sphinx* sp. are not found below 1000 metres altitude south of 25°N latitude (the species is found as south as 15°N latitude in Thailand; some records have no altitude information, but the locations are usually in mountainous regions). However, some species of the genus *Pinus*, which is frequently recorded as a host plant genus for *Sphinx* moths, do naturally occur in some lowland areas such as Sumatra, Luzon and Mindoro, where *Sphinx* are not found.

Among the 'restricted range' distribution class only one potential candidate was found: *Eupanacra malayana* is recorded to feed exclusively on Hypoxidaceae (three records, all genus *Curculigo* from Java and the Malay Peninsula). The host plant family is distributed in the Southern hemisphere and tropical Asia, whereas the moth occurs from Sikkim in the Indian Himalaya foothills eastwards to the Wallace line, on the Lesser Sunda Islands a little beyond that to Sumbawa (Beck & Kitching 2004). There is therefore a possibility that the moth is limited in its Northern distribution by the range of the host plant, but a direct influence of climate might as well produce the observed distribution. There is no host plant family range that would explain any of the prominent biogeographic boundaries of Sphingidae within the Malesian archipelago, such as Wallace's line (see chapter 4.1).

Smerinthinae are the only group that feeds on Dipterocarpaceae, the dominant canopy tree family in Southeast-Asian lowland primary forests (Whitmore 1990, Slik et al. 2003). Records come from three species (*Ambulyx canescens, A. substrigilis, Cypa decolor*), of which the two *Ambulyx* are commonly encountered in primary lowland regions on Borneo. *A. canescens* might even be quite specialised: Four out of four records come from various Dipterocarpaceae tree species in Southeast-Asia. This species is another example of a potentially congruent northern limit of host plant and moths, which might be a consequence of a common constraint (e.g. temperature), rather than a cause and effect (as discussed above).

Three species of Macroglossinae are feeding on grasses (Poaceae), a plant family that in tropical Southeast-Asia is probably mainly found in highly disturbed areas (except of bamboo).Two of them are extremely widespread in the old world tropics (*Hippotion celerio*) and the Palaearctis (*Hyles livornica*), whereas the third (*Hippotion brennus*) is an Australasian species (see Beck & Kitching 2004 for details). Furthermore, two *Leucophlebia* species (Smerinthinae) from continental Asia are recorded exclusively from Poaceae. Most Poaceae records come from agricultural plants, only *L. emittens* is recorded from bamboo.

Fabaceae are among the five most commonly recorded Sphingid host plant families, 18 hawkmoth species are known to feed on this family. This emphasises the potential of hawkmoths as agricultural pests; *Clanis bilineata* caterpillars, for example, are a common pest on bean fields in China (I.J. Kitching pers.com; see also Poaceae feeding above and Moulds 1981, 1984).

Discussion

Biases due to incomplete and erroneous data

Food plant records for tropical Lepidoptera are generally incomplete – even for the well-sampled butterfly families Papilionidae, Pieridae and Nymphalidae, life-history information is available only for ca. 50 percent of the species in Malaya and Borneo (Fiedler 1998). It must be assumed that locally common, widespread species have a higher chance of being investigated. Furthermore, much of the host plant data stem from relatively old sources (i.e., almost 45 percent of records on Sphingidae were published earlier than 1950), often from expatriate European non-professional lepidopterologists, which might bias records in favour of those species occurring in the garden areas of former British colonies (the latter bias can be confirmed from the location of records, as well as from the distribution of presence-only records for Southeast-Asian hawkmoth species, see e.g. Beck & Kitching 2004). Furthermore, the completeness of the host plant range of species might be biased along the same gradients – it is unlikely that the host plant range of a species from primary forest on a logistically or politically inaccessible area (e.g. central New Guinea) is as well known as that feeding on garden ornaments in former colonial strongholds (e.g. Australia, 'hill stations' of India &

Malaya). The use of higher taxonomic units of host plants helps to diminish effects of undersampling, but a dependence of recorded host plant families and even HTOs is still evident in data (figure 5.4). However, the true magnitude of these biases is extremely difficult to assess or correct, as species with an ecological preference for disturbed areas (e.g. gardens) might actually have a wider geographical range and be more generalist than primary forest specialists (compare e.g. to Wilson 1961 for ants, Glazier 1980 for rodents). Thus, all conclusions from this analysis must be treated as preliminary and tentative, as the above mentioned biases have the potential to produce artefact results: Smerinthinae, for example, appear to be less abundant and less specious in anthropogenically disturbed areas (chapter 3.1) and are apparently less polyphagous than other subfamilies.

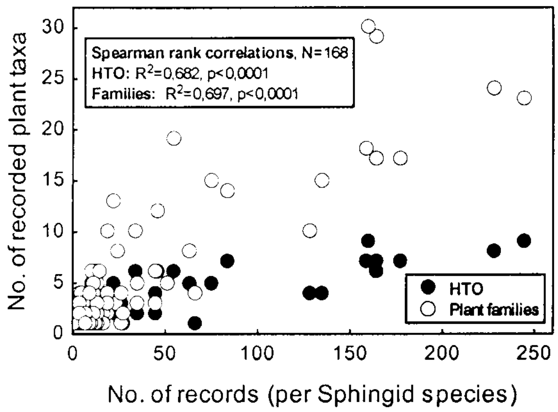


Figure 5.4 shows the increase of recorded taxa with increasing number of records. Both HTO and plant family data are correlated with the number of records.

Errors in host plant data are common in the Lepidoptera literature (see e.g. Fiedler 1998 for discussion and references on butterflies) and might refer to misidentification of the moth, the plant, or wrong information on the location. All data for 'confirmed' errors were excluded from analysis, while ca. 2,5 percent of the utilised data were unconfirmed or questionable (I.J. Kitching pers. com.). Thus, erroneous reports might certainly still be contained in data, but probably not in a frequency that could produce serious biases.

Differences between taxonomic groups

Subfamilies and tribes differ in the number of plant families that are utilised per moth species and even show strong trends to differ in the number of Higher Taxon Orders (*sensu* APG 1998). Particularly some species of the subfamily Sphinginae are recorded on a large number of plant taxa, some of which are not used by any other oriental Sphingidae (figure 5.2). Comparisons of the frequency of monophages, oligophages and polyphages (on plant family level) indicate the same trend, although figures are not statistically significant.

The diversity (as measured by Fisher's α, figure 5.3) of utilised plant families for whole subfamilies (or tribes) shows a different trend: The subfamily Smerinthinae is recorded on a more restricted number of plant taxa than other subfamilies, although average host plant families per species do not differ from that of Macroglossinae (figure 5.1). Thus, if this result is not a sampling artefact (which would be rather expected with the absolute number of plant taxa per species, not with diversity for the subfamily, see above), it must be concluded that some ecological or phylogenetic constraint is limiting the diversification of Smerinthinae host plant choice. Phylogenetic conservatism in the adaptation of herbivores on plant secondary compounds, for example, can have a big influence on insect-plant interactions (Mitter et al. 1991, Farrel & Mitter 1993, Miller & Wenzel 1995).

Holloway (1987a) suggested in analogy to Janzen (1984) that the host plant utilisation of Smerinthinae *vs.* Macroglossinae & Sphinginae on Borneo does not overlap much. This lack of overlap could not be confirmed in this more extensive data set, Smerinthinae host plant use seems rather nested within that of Macroglossinae. Interestingly, Holloway (1987a) argues that the discrepancy between the 'slight overlap' in his data (Bornean species, but host plant data of these species from their Indo-Australian range) and the strict separation in host plant families in Janzen (1984) may be a result of the larger geographical scale of host plant data acquisition. If this is correct for whatever reason – incompleteness of data from small scales or local adaptation of communities –, it might explain that data for Southeast-Asian species, using global host plant data for these species, produces even more overlap between subfamilies.

No comments can be made here about the quality of host plants, e.g. if there are common traits (in structure or chemistry) among the Smerinthinae food plants. Possibly, Smerinthinae utilise trees more often than other subfamilies (Schulze 2000, referring to Holloway 1987a), which is a common trait among species with reduced proboscis (Miller 1997). If so, patterns of diversity along habitat gradients on Borneo (see chapter 3.1, Schulze 2000) might be well explained: Smerinthinae are most divers in primary forests, where obviously many trees are found, and in montane zones, where reduced tree diversity makes it easier to find the appropriate host species (Schulze 2000). However, host plant data await further analysis to confirm or reject this hypothesis.

Janzen (1988) suggests that species with long lists of host plant records might actually be fairly specific under local conditions, but accumulate a lot of records over their wide geographical range (i.e., their *fundamental niche* is much wider than their *realised niche*, Fiedler 1998; see Kawecki & Ebert 2004 for theoretical aspects of local adaptation). Generally, geographic variation in local resource utilisation behaviour is known from a number of animal species (e.g. Foster 1999). Furthermore, browsing Janzen & Hallwach's (2004) online-databank on Sphingidae caterpillar's host plant records from Costa Rica (a relatively small country) gives the impression that most species are quite specific to one or two plant families. Host plant feasibility for an herbivore insect can differ significantly between regions (even within the same host plant species) on a much smaller scale than considered here (Mody 2003). Indeed, species with a wide variety of recorded host plants appear to be more wide-spread than host-specific species (see chapter 6), but the reason for this relationship might also be the other way around: Polyphagous species might be able to extend their range more easily than host-specific moths (Gaston et al. 1997).

Data for Southeast-Asian Sphingidae caterpillars with feeding records on a large number of plant families do not support the idea of local specialisation for the four species with the largest number of recorded host plants (23-30 families), although a quite broad definition of 'local' was used: Mean host plant families per country were calculated, using only countries with at least four records. The huge country China was treated as two regions, applying a North-South separation, while no such separation was possible for Australia and India due to many unlocalised records in the original data. Indonesian records were exclusively from the western part (Java & Sumatra). Data of host plant families per country are (Mean ±SD [N: number of countries]): *Hyles livornica*: 4,78±1,99 [N=9], *Acherontia lachesis*: 6,60±4,09

[N=10], *Hippotion celerio*: 4,53±2,07 [N=15], *Agrius convolvuli*: 2,28±1,07 [N=18]. Thus, three out of four species would still be judged polyphagous on country level even though undersampling biases are evident in data (often four records refer to 3-4 host plant families). Only *A. convolvuli* appears far more restricted in its country-wide feeding than over its global range. On country level, the species is typically reported on Convolvulaceae plus one or two additional plant families, which change between countries.

Similarly, two species with a valid subspecies distinction (Kitching & Cadiou 2000), sufficient sample size and host plant heterogeneity were analysed for differences in the host plant choice of subspecies. For *Theretra latreillii* (see distribution maps in Beck & Kitching 2004) eleven host families are recorded, whereas ssp. *latreillii* is recorded on six families and ssp. *lucasii* on ten families (five plant families are shared). Thus, both subspecies separately would still be considered polyphagous. The same applies to *Theretra oldenlandiae* (15 host plant families), with ssp. *oldenlandiae* recorded on 13 plant families and ssp. *lewini* on nine families (seven families shared). Under the assumption that the number of records in the data bank reflects the preference of moth taxa for a certain plant family (which is highly unconfirmed, see discussion on data biases above), frequency tables of *subspecies* x *plant family* can be tested for non-random differences, which would be an indication of local adaptation. No significant effect was found for *T. latreillii* (N=76, $\chi^2_{df=10}$=10,64, p=0,384), while there is a difference in *T. oldenlandiae* (N=153, $\chi^2_{df=15}$=35,78, p=0,001).

Novotny et al. (2004) suggested in an analysis of New Guinean caterpillar communities that local food plant adaptation might be very specific for most species, supporting the idea of 'geographic accumulation' of food plant records in far-ranging species despite local monophagy. However, it might be worth comparing such studies to temperate European examples, where 250 years of forest zoology and pest control produced a far better understanding of host plant relationships of herbivorous insects: For example, as most species in Novotny et al.'s (2004) New Guinean community, >90 percent of caterpillars of the geometrid species *Operopthera brumata* and *O. fagata* are found in most years on Oak (*Quercus* sp.), respectively Beech (*Fagus* sp.) trees (K. Fiedler pers. com.). However, both species have the potential to feed on very different plant taxa as well (particularly if the normal hosts are not available, e.g. in years of oak defoliation by pest insects), which becomes evident in forests with a higher diversity of deciduous trees, blueberry undergrowth, or on apple and cherry plantations, where *brumata* can be a pest. Some other studies on widespread, polyphagous butterflies also failed to find local host adaptation despite favourable conditions for its evolution (Wehling & Thompson 1997, Bergström et al. 2004 and references therein), possibly because variable habitat conditions exhibit selective pressure to retain the ability of utilising alternative hosts (Bergström et al. 2004). Thus, it makes a difference if the matter of 'polyphagy' is viewed from the plant's perspective (where certain insects species appear as fairly specialised predators) or the herbivore's perspective, where some are truly monospecific by behavioural or physiological constraints, whereas others have the potential to switch host if the conditions make it advantageous. Ward & Spalding (1993) noted in a thorough analysis of the known host plant relationships of British phytophagous arthropods that, unlike most other arthropod taxa, the larger-bodied Lepidoptera families contain a relatively high proportion of polyphagous species (i.e., ca. 50 percent of the species are feeding on ≥3 plant families).

Host family range as a limiting factor for moth range

No evidence or even indication could be found for the hypothesis that host plant range is a limiting factor for Sphingidae distribution with the preliminary, 'quick and dirty' approach that was presented here, matching the conclusion of Quinn et al. (1997, 1998) on British Lepidoptera). Rather, food plant presence is a necessity for moth presence, but other factors such as climate or dispersal barriers usually keep the moth's range considerably smaller than the combined range of its host plant families. However, it should be kept in mind that a more careful approach, including a more thorough compilation of host plant distribution records and subsequent GIS-based analysis might bring further and more detailed insights, but this is beyond the scope of the work that is presented here. Furthermore, it might be argued that the *a priory* assumption of plant family as the relevant taxonomic unit of host plant specialisation might be wrong. As a first assessment of this objection those species were filtered out, which are recorded as monophagous on one plant family, but for which at least five host plant records were available (in order to avoid undersampling-biases). Of these 23 Sphingid species, it was counted how many genera and species within their host plant family were recorded as larval hosts. Means±SD were 4,3±2,5 for plant genera and 7,0±3,7 for species, so specialisation on a genus or even species appears uncommon. In this data, only two cases of plant genus specialisation were observed: *Hippotion rafflesii* is only recorded from *Impatiens* (Balsaminaceae, 7 records), and *Nephele hespera* seem to feed only on *Carissa* (Apocynaceae, 8 records). Novotny et al. (2002c), on the other hand, report of a large number of various insect taxa which feed on various plant species *within* the same genus under local conditions.

CHAPTER 5.2 - THE DISTRIBUTION OF BODY SIZES

Abstract

Body sizes of 281 Southeast-Asian Sphingidae were measured as mean forewing lengths and were used to explore 1) the shape of the regional frequency distribution of body sizes, 2) the frequency distribution of body sizes in local assemblages, 3) differences in species' size between different subfamilies, habitats and regions, and 4) the spacing of body sizes between species.

The Southeast-Asia-wide frequency distribution is slightly right-skewed (i.e., there are more small species than large ones) and can be described by a lognormal distribution. However, the distribution is bimodal, which is probably caused by systematic size differences between the subfamilies Macroglossinae and Smerinthinae.

Local assemblages do not show a consistent skew and can be fitted by a normal distribution. No consistent effects of habitat or region could be found to explain differences in mean species size between local samples, which were nevertheless observed.

The distribution of body sizes does not show any regularities that would indicate competition effects, but rather suggests that body sizes might be 'clumped' due to a common constraint on the evolution of Sphingid body sizes.

Introduction

The distribution of animal body sizes is – on a large scale – a pivotal parameter to make a connection between biogeochemistry (the flow and transformation of matter and energy in ecosystems, Begon et al. 1996) and community ecology. Many general theories (e.g. Hubbell 2001, Maurer 1999, Ritchie & Olff 1999) give consideration to the rules of how a given resource is translated into many small-bodied or few large-bodied individuals (see e.g. Blackburn et al. 1992 and references therein), and what consequences this has on ecosystem functions (e.g. Makarieva et al. 2004). This trade-off is a major evolutionary constraint within species as well as in species communities (e.g. Stearns 1977, cited and reviewed in Begon et al. 1996). The global interspecific distribution of animal body sizes appears strongly right-skewed (more species are small-bodied), but with a decline towards the very small body sizes (Blackburn & Gaston 1994, Rosenzweig 1995). The reasons for the shape of this curve are not fully understood – particularly if the decline in species numbers at very small body sizes is an effect of undersampling (see e.g. Blackburn & Gaston 1998) or if it has biological reasons such as declining habitat heterogeneity at very small scales (Rosenzweig 1995, see Siemann et al. 1996, Gaston et al. 2001 for empirical studies). On a smaller taxonomic scale, constraints on the functioning of a taxon-specific *bauplan* strongly limit the body size distribution around a taxon-typical size, whereas adaptation to different habitats or life-styles leads to variation from this medium value (e.g. Siemann et al. 1996). Competition can influence interspecific body size variation as many niche dimensions are probably related to body size (Begon et al. 1996). Based on the premises of fractal habitat parameters (such as the distribution of food patches; Burrough 1981, Bolliger et al. 2003) and a lower tolerance of small animals to low food quality or density (due to higher respiratory rates), Ritchie & Olff (1999) showed that a 'spatial scaling' model leads to the expectation of a left-skewed body size distribution in local assemblages of animals with similar feeding habits.

Interspecific variation of body sizes has been associated to a number of other macroecological parameters (besides species richness, see above): Large species are less common than small species in local assemblages (Hodkinson & Casson 2000, Maurer 1999, Basset & Kitching 1991, but see Morse et al. 1988), they have larger ranges (Biedermann 2003, Olifiers et al. 2004) and in Lepidoptera (as well as some other taxa) they have a lower feeding specificity (Loder et al. 1998 and references therein, Gaston & Reavey 1989, Ward & Spalding 1993, Wasserman & Mitter 1978).

Here, the frequency distribution of body sizes of Southeast-Asian Sphingidae is investigated. In particular, the shapes of the distribution for the regional assemblage as well as for a number of local assemblages are compared. Furthermore, mean body sizes between subtaxa and between different habitats are compared and the size ratios of species are analysed for effects of competition in the community.

Methods

Body size is theoretically best measured as body mass, but in practice volume or length are often used as they are easier to measure and usually correlate well with body mass (Schoener 1980). Forewing lengths (FWLs) are good indicators of Lepidopteran body size as long as they are used within groups of similar body architecture (e.g. Loder et al. 1998, Schoener 1980). Adult size is considered as a decent estimator of larval size (Gaston & Reavey 1989). FWLs of Southeast-Asian Sphingidae were measured with a calliper during light trapping sessions in Malaysia and Indonesia (see appendix I for sampling sites). Mean values for species were calculated if more than one specimen was available, using only male specimens, which are far more frequent in light trapping samples (e.g. Brehm 2002). Males are smaller than females in some sexually dimorphic species. Further data for mean value calculations of Philippine species were taken from Treadaway (2000). Additionally, FWLs of single specimens were measured in D'Abrera (1986), who pictures hawkmoths in original size, and from the collection of the Natural History Museum, London. All together, data from 6.839 specimens provided size information for 281 of 380 species in Southeast-Asia (Beck & Kitching 2004). Specimen numbers per species ranged from singletons to 491 specimens. Data for 201 species (72%) stem from less than 10 specimens, for 149 species (53%) only singleton data were available.

Data of light trapping of local assemblages stem from a compilation of own samples, published data (Chey 1994a, 2002, Holloway 1976, Schulze 2000, Tennent 1991, Zaidi & Chong 1995) and unpublished sources, which are described in detail in chapter 3.1 (e.g. table 3.1). The method of Hochberg (1988) was used to control for spurious results from multiple test in the same data set. Failures of tests in passing these criteria are noted in the text.

Results

Body size distribution of Southeast-Asian Sphingidae

Mean forewing lengths of 281 Southeast-Asian hawkmoth species range from 14 millimetres (*Sphingonaepiopsis pumilio*) to 72 millimetres (*Clanis pratti*, see Beck & Kitching 2004 for pictures of all species), the median FWL is 36,2 millimetres. The frequency distribution of FWLs is bimodal (figure 5.5a) due to systematic differences between the subfamilies (figure 5.5b). However, a lognormal curve is not rejected as a distribution model.

Body sizes of log-transformed FWLs differ significantly between subfamilies (figure 5.6), Macroglossinae are (on average) significantly smaller than Smerinthinae or Sphinginae. On the next lower taxonomic level, no differences of tribes within the subfamilies Macroglossinae and Sphinginae can be found, while within the Smerinthinae species of the tribus Ambulycini are significantly larger than those of the tribus Smerinthini (Anova, Fisher's LSD *post hoc* test: p<0,001). A strong influence of phylogeny on a

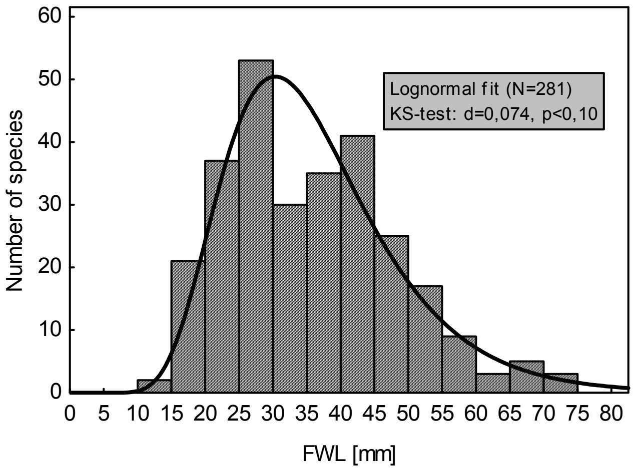


Figure 5.5a shows the frequency distribution of Sphingidae forewing lengths for 281 Southeast-Asian species. Data is reasonably fitted by a lognormal distribution.

conservative trait such as body size must be expected (Harvey & Pagel 1991, Schmidt-Nielsen 1984, Begon et al. 1996, Webb et al. 2002).

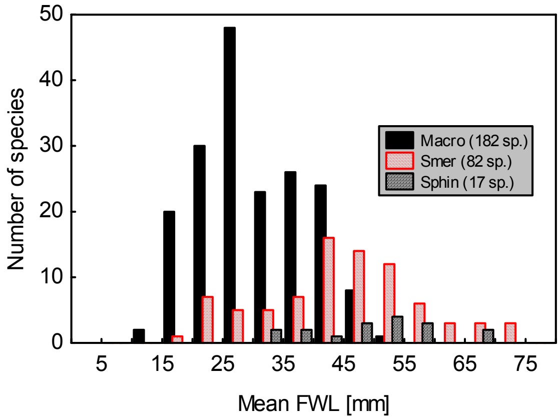


Figure 5.5b: Frequency distribution of Sphingidae forewing lengths, separated by subfamilies. Sphinginae and Smerinthinae data can be fitted by a normal distribution (KS-test, $p>0,20$), whereas the subfamily Macroglossinae still exhibits an extraordinary peak at the size class between 25-30 mm FWL, mainly due to the genus *Macroglossum* (KS-test for normality: $D=0,114$, $p<0,05$). An exclusion of the genus *Macroglossum* still leaves a peak between 25-30 mm (not shown), but data can be fitted by a normal distribution (KS-test: $D=0,079$, $p>0,20$).

A number of genera (*Macroglossum, Cephonodes, Hemaris & Sataspes*) are mostly day-active and might thus be considered as not belonging to the night-active Sphingid guild. Furthermore, all day-active Sphingidae are relatively small, and all but four species (*Sataspes* sp.) belong to the subfamily Macroglossinae. One could suspect that the bimodality and right-skew of the frequency plot (figure 5.5) as well as the smaller average size of Macroglossinae (figure 5.6) is caused by these species. An exclusion of day-active taxa leaves 197 species in analysis. Their frequency distribution looses its right-skew and is better fitted by a normal (KS-test: $d=0,054$, $p>0,20$) than by a lognormal distribution (KS-test: $d=0,076$, $p<0,20$). However, bimodality remains (data not shown) with local peaks occurring at 25-30 and 40-45 millimetres FWL. Furthermore, even after exclusion of the numerous small *Macroglossum* species (as well as other day-active taxa), Macroglossinae are significantly smaller than the other subfamilies (Anova: $F_{df=2}=33,99$, $p<0,0001$).

Body size distribution in local samples

FWLs of all recorded species were available for 43 local light trapping samples with sample sizes ≥50 individuals. Samples stem from Peninsular Malaysia, Flores, Seram, and, in majority, from Borneo. Individual numbers of the local samples range between 56 and 1.748, local species numbers between 10 and 50. Some frequency distributions of the FWLs of species in local samples are left-skewed, some are right-skewed (figure 5.7), but none deviates significantly from a normal distribution models (KS-test: $p>0,20$).

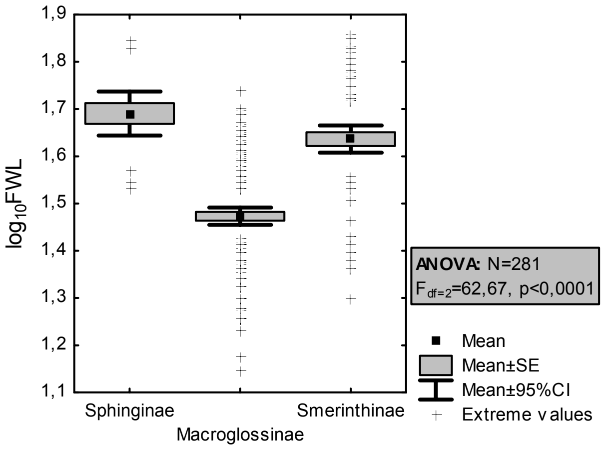


Figure 5.6 shows mean values for (log-transformed) forewing lengths of Sphingidae subfamilies. ANOVA *post hoc* tests (Fisher's LSD) reveal highly significant differences between Macroglossinae and the two other subfamilies.

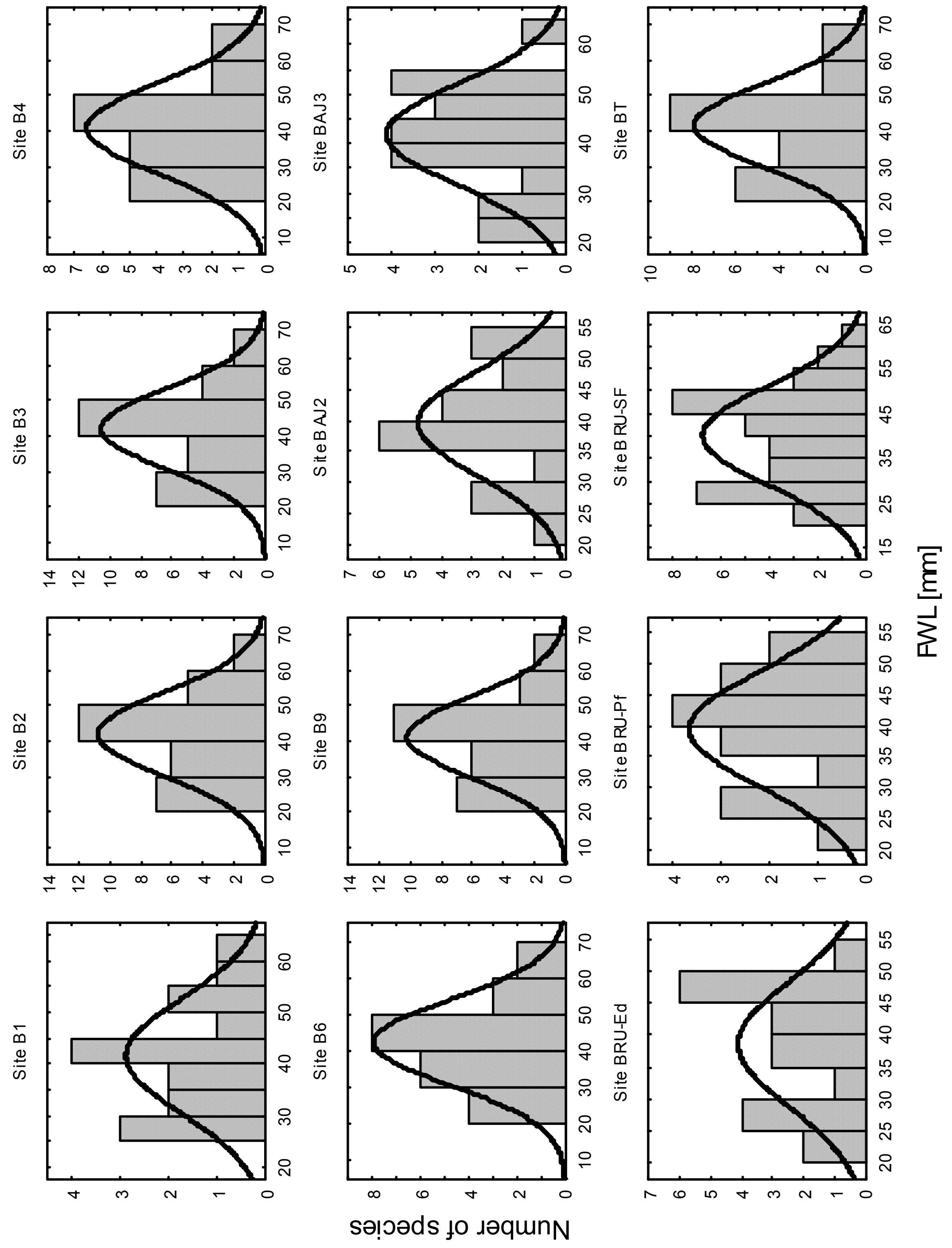
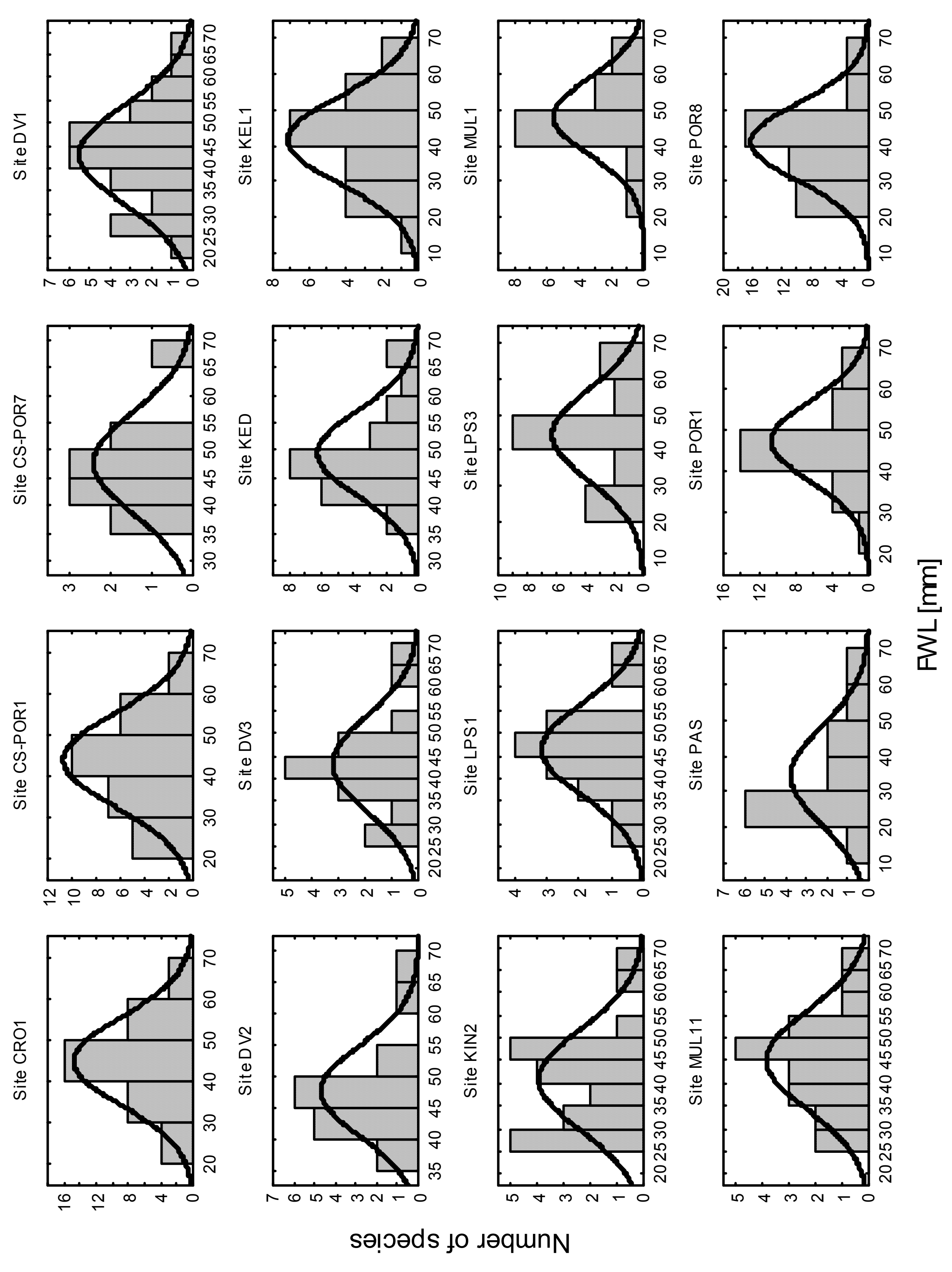


Figure 5.7 shows local FWL-distributions at 43 light trapping sites (≥50 individuals, alphabetically sorted acronyms, see appendix **I**). Very rarely occurring day-active taxa (*Macroglossum* sp.) were excluded from data.



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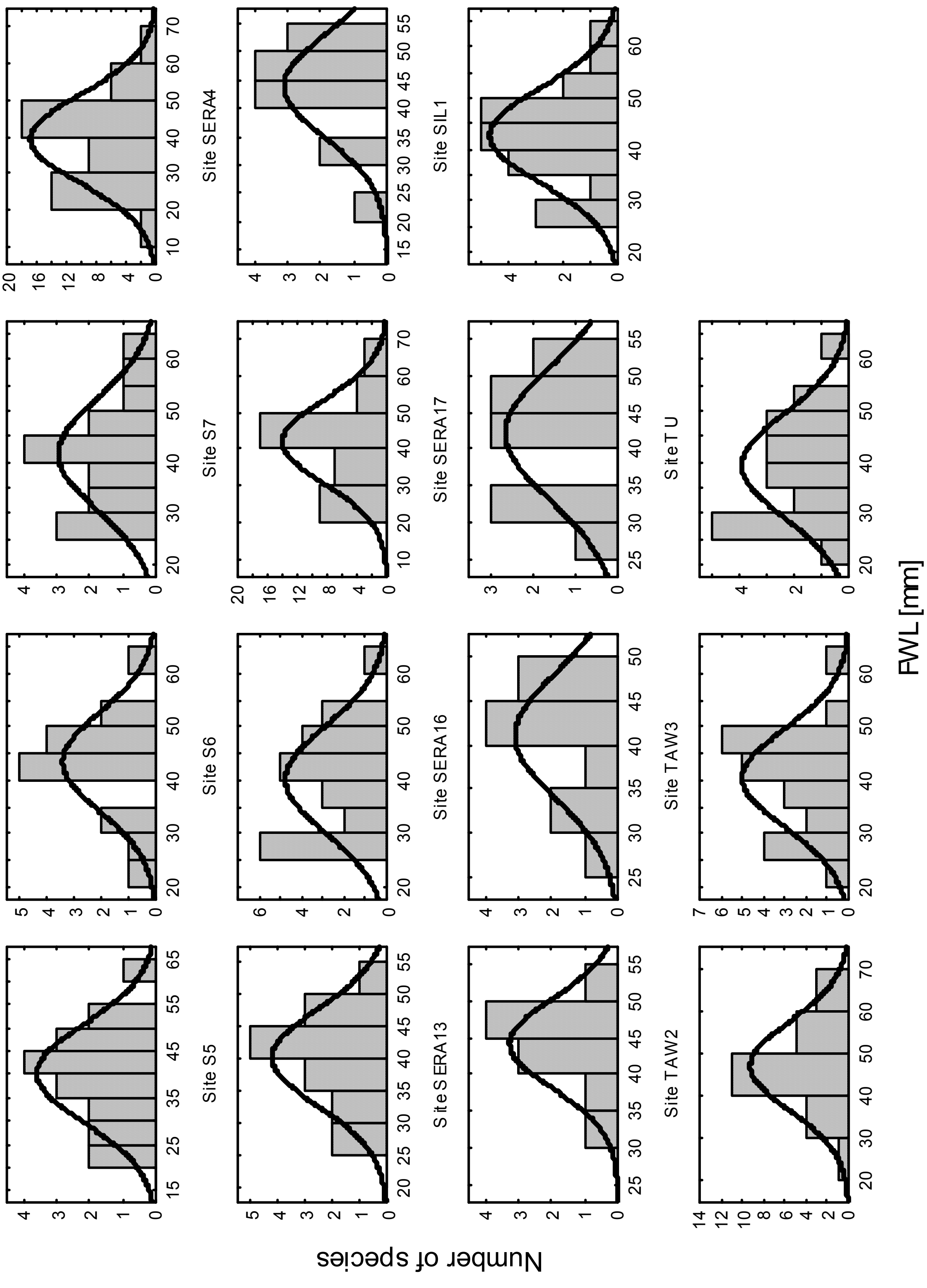

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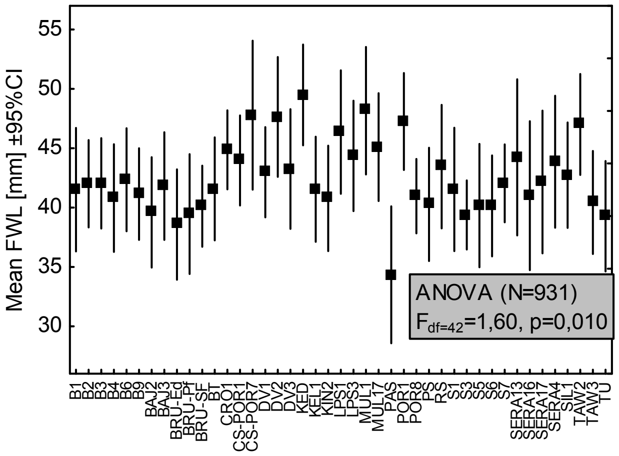


Figure 5.8 shows means of species' FWLs for 43 local assemblages from Peninsular Malaysia (KED, PAS), Flores (BAJ2, 3, KEL1), Seram (SERA4, 13, 16, 17) and Borneo (all others). See appendix I for site details.

Figure 5.8 shows mean FWLs of species for each site. Significant size differences between the sites were found, but cannot be clearly associated with differences in region or habitat. The sites with the largest and the smallest mean FWL sizes are both from Peninsular Malaysia. A generalized linear model (GLM: Guisan et al. 2002, StatSoft 2003) was used to test the influence of habitat disturbance (in three classes, see chapter 3.1) and altitude on mean body sizes. The model is very weak (R^2=0,009, p=0,046) and does not pass the criteria of Hochberg (1988). Futhermore, univariate significance tests are not significant, neither for altitude ($F_{df=1}$=1,44, p=0,231) nor for disturbance ($F_{df=2}$=2,14, p=0,118). The local distributions of FWLs of individuals (instead of species) have generally a similar pattern as that of species (see also Siemann et al. 1996, Morse et al. 1988), but are more irregular than the latter. Three-dimensional plots (figure 5.9), showing the number of species in different size- and abundance classes (the latter in $\log_2$-classes), are

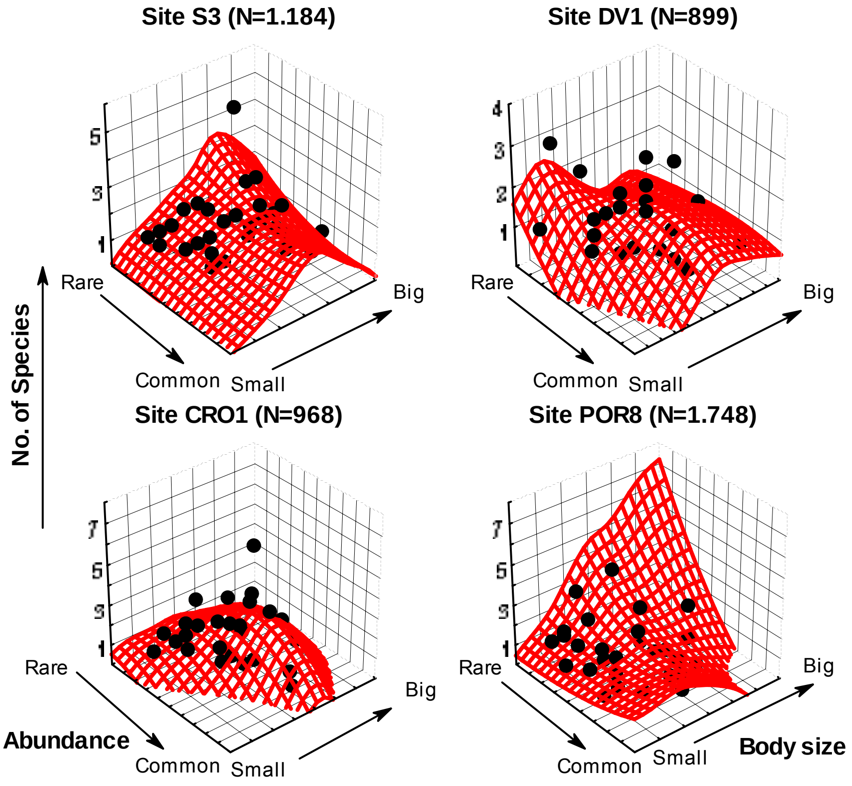


Figure 5.9 shows 3-dimensional plots of species and individuals (in octaves) per size class for four local light-trapping samples from Borneo >850 specimens. Surfaces were fitted by the *negative exponential least square* method.

displayed for several large local samples (>850 specimens, all from Borneo), for which undersampling of rare species should be minimal. At one site (S3) the fitted surface (*neg. exp. least squares*, StatSoft 2003) matched the pattern found in other studies (e.g. Geometridae from Borneo: Beck 1998, beetles on rainforest trees: Morse et al. 1988, Basset & Kitching 1991); i.e., most species are rare and of medium size. Surfaces are more irregular in the other sites, with a bimodal distribution pattern in DV1.

Ratios of body size as indicators of community structure

The mean ratios of neighbouring FWLs were compared at four sampling sites in Borneo with more than 250 individuals, for all Sphingidae as well as for the three subfamilies separately. Sampling habitats covered a primary forest (DV1), a selectively logged forest (DV2), and an agricultural site (POR8) in the lowland as well as a montane forest site at ca. 1200m a.s.l. (CRO1, see appendix I for details on all sampling sites). As figure 5.10 shows, mean ratios were between 1,04-1,12. Thus, they are clearly below the ratio of about 1,3, which would be expected if FWL size was a selected niche dimension (Hutchinson 1959, cited & reviewed in Begon et al. 1996). Effects of competition would be expected to be strongest among closely related species. Mean ratios for taxonomically closer related groups (subfamilies) appear to be higher than for all Sphingidae, but this difference is not statistically significant. Due to sample size restrictions, no reasonable comparison could be carried out at lower taxonomic levels.

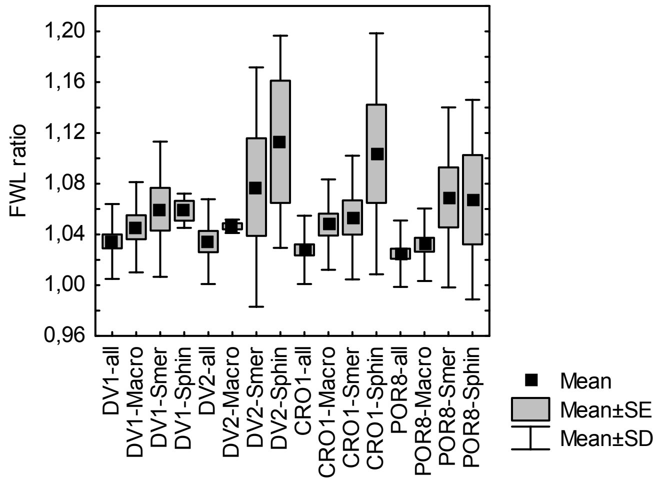


Figure 5.10 shows mean FWL ratios of neighbouring size ranks for all Sphingidae, as well as separately for the three subfamilies Macroglossinae, Smerinthinae and Sphinginae, at four sites, respectively, in Borneo.

From a model of spatial scaling Ritchie & Olff (1999) predict lower size ratio, hence more body size overlap, in large species from local assemblages. It might therefore be suspected that the normalisation of the body size distribution in local assemblages (figure 5.7) from a lognormal body size distribution in the taxon (figure 5.5a) is caused by a reduction in small species that leads to higher body size ratios. Body size ratios of small (FWL≤median) and large (FWL>median) species pairs were compared for all species and three local assemblages (DV1, POR8, CRO1). Congruent with Ritchie & Olff's (1999) ideas, small species generally had a higher body size ratio than large species (despite a right-skewed, instead of left-skewed frequency distribution), but the difference is found in the data for all species (M.-W. U-test: Z=-2,208, p=0,027) as well as that of the local assemblages (U-tests, p=n.s.).

A null-model simulation analysis of the 'segment lengths', which are cut by mean FWLs in the local assemblages, was carried out with the computer program *EcoSim 7.58* (Gotelli et al. 2003). Observed segment lengths are compared to those from a random simulation (within the limits of the observed data) to assess if they are more or less evenly spaced than would be expected by chance (Gotelli et al. 2003). Significantly smaller observed values would indicate biotic structuring (competition) within the community, whereas larger observed values would indicate that species share common constraints on body size. No effects of competition structuring could be found (see table 5.3 for results), while on the agricultural site (POR8) there is indication of a body size constraint. For log-transformed FWL ratios, which measures size-ratio rather than absolute size differences, no significant results were found, as is the case for separate analyses of the subfamilies Macroglossinae and Smerinthinae (local species numbers of Sphinginae were too low for simulation analysis).

	Obs. Ind.	Sim. Ind.	Var (sim.)	p
DV1	1,537	1,910	0,383	0,716
DV2	3,163	2,690	1,528	0,264
CRO1	1,578	1,576	0,235	0,422
POR8	1,820	1,122	0,109	0,030

Table 5.3 gives results of a null model simulation (*EcoSim*, Gotelli et al. 2003, no transformation, otherwise default settings) of the variance of segment lengths FWL ratios. Observed indices that are smaller than randomly generated indices suggest an effect of competition on the structuring of body size variance, while observed values greater than the simulated ones indicate a common constraint on body sizes. P-values indicate the significance of the respective effect.

Discussion

Data biases

Data for Southeast-Asian Sphingidae covered 281 of 380 species (74%) in the region. Missing species were typically very rare and often only recently described (thus, not contained in D'Abrera 1986). The reported local distributions, on the other hand, are probably fairly complete with regard to night-active taxa (see chapter 2) at least for the largest samples (e.g. DV1, S3, POR8, CRO1, see figure 5.7), but systematically exclude taxa that do not come to artificial light sources at night. Differences in the shape of the regional and local body size distributions could therefore be caused by one or the other of these biases, or they could be genuine.

The general body shape of Sphingidae is certainly uniform enough to justify the use of wing length as an allometric measure of body size, yet there are differences in body shape between subfamilies which could bias these measurements slightly: On average, Macroglossinae are a more 'sturdy' in body shape than Smerinthinae, resulting in a higher *thorax:FWL* ratio ('wing load') in the former subfamily: From a collection of Bornean samples, one male individual per species was randomly chosen and measured. Average wingloads ($\text{Mean}_{\text{No.Spec.}}$±SD [mm]) for Macroglossinae are $0{,}243_{31}$±0,039, for Smerinthinae $0{,}194_{11}$±0,015 and for Sphinginae $0{,}226_{5}$±0,040. An ANOVA indicates significant results ($F_{df=2}=7{,}03$, $p<0{,}01$), Fisher's LSD *post hoc* tests show a significant difference between Macroglossinae and Smerinthinae ($p<0{,}0001$), while they are non-significant for other pair-wise comparisons. Therefore, the body mass of Macroglossinae could be slightly underestimated by FWLs, while that of Smerinthinae might be slightly overestimated. The exclusive use of male specimens for FWL measurements, on the other side, underestimates body masses of Smerinthinae and

Sphinginae, where sexual dimorphism in size (with larger females) could be observed (e.g. *Ambulyx pryeri, Psilogramma menephron*). However, only among the common species females were regularly caught at light, so the use of mean values for male and female specimens would have biased results in a rarity-commonness dimension.

Distribution of body sizes

Most body size distributions were reported as unimodal (Siemann et al. 1996, and references therein) and more or less strong right skewed (Blackburn & Gaston 1994a, b, Gaston et al. 2001, but see Ritchie & Olff 1999 for left-skewed examples), although taxonomic sub-groups (e.g. insect orders) have their frequency maxima at different sizes (Basset & Kitching 1991, Siemann et al. 1996). With a ca. five-fold increase from the smallest to the largest species, the range of body sizes of Southeast-Asian Sphingidae is, in comparison to other studies and taxa (e.g. Siemann et al. 1996, Morse et al. 1988, Basset & Kitching 1991), very low – Sphingidae are relatively tightly distributed around the medium hawkmoth size. Despite this and the relative low taxonomic classification as a family, clear and significant differences in body size were observed between subfamilies (figure 5.6), and it must be suspected that the overall right-skewed, bimodal shape of the body size distribution (figure 5.5a) is caused by these differences. Indeed, separate frequency plots for subfamilies (figure 5.5a) reveal a unimodal right-skew for Macroglossinae and a weak unimodal left-skew for Smerinthinae, as well as for the small subfamily Sphinginae. A similar cause for bimodality in a complete animal assemblage was reported by Gaston et al. (2001) due to different peaks in vertebrates and invertebrates.

This subfamily dichotomy of Macroglossinae *versus* Smerinthinae and Sphinginae is unusual in the light of other findings on Southeast-Asian Sphingidae: Major dichotomies in local abundance and species richness (Schulze 2000, chapter 3.1) and biogeography and dispersal (chapter 4.1) were found between Smerinthinae on the one side, and Macroglossinae and Sphinginae on the other side, and were tentatively discussed in connection to life-history differences in the adult's acquisition of resources (Lemaire & Minet 1998, see also chapter 1.2).

Phylogenetic effects on body size must always be expected (Begon et al. 1996, Webb et al. 2002, Schmidt-Nielsen 1984), on the level of subfamilies as well as on lower taxonomic levels. Thus, phylogenetic controls are a standard practice in comparative studies regarding body size (e.g. Harvey & Pagel 1991, Garland et al. 1999). However, relevant statistical tests did not yield significant results even for raw data, which made it unnecessary to apply correction procedures such as independent contrasts (e.g. Harvey & Pagel 1991), which usually produce results at lower significance levels than raw data analyses (Garland et al. 1999). Among the Macroglossinae, the genus *Macroglossum* is exceptionally species-rich (76 species in Southeast-Asia, FWL data were available for 55 species) and might bias subfamily comparisons of mean sizes and distribution shapes. However, even with exclusion of *Macroglossum* sp. (see above), size differences among subfamilies persist and the frequency distribution of Macroglossinae remains left-skewed, albeit less strong.

At a local level, where light trapping as sampling method generally excluded *Macroglossum* as well as some other small, day-active taxa, distributions appear not skewed (figure 5.7), although smaller sample sizes might also hide such effects. However, if individual numbers (instead of species richness) are considered (not shown) a trend to bimodality of size distribution can still be observed in local assemblages.

No directional effects of habitat parameters on the distribution of body sizes were observed, which agrees with results from geometrid moths on a habitat gradient in Borneo (Beck 1998). Differences between single sites were observed (figure 5.8) and it might be expected that they are caused to a certain degree by phylogenetic effects, e.g. different faunal composition that favours larger or smaller taxon groups (Webb et al. 2002). However, as the differences do not follow any interpretable pattern (i.e., differences in the island, habitat disturbance, or altitude), no attempts were made to quantify the phylogenetic independence (e.g. Freckleton et al. 2002, Abouheif 1999) or to correct data for site comparisons (e.g. Harvey & Pagel 1991).

Competition and constraints

Adult body sizes, which were also used before as indicators of larval size in Lepidoptera (Loder et al. 1998), do not show any indication of being a competition-selected niche dimension. Neither size ratios of neighbouring rank nor null-simulation analysis showed that body sizes are spaced in a systematic way, which would suggest competition effects. Effects of competition on herbivore insects, particularly in the tropics, have generally been considered weak (Gurevitch et al. 1992, Strong et al. 1984, but see Denno et al. 1995) and communities in high-productivity regions are more likely to be governed by predation (incl. parasitism; Strong et al. 1984, Gurevitch et al. 2000, see also Bohannan & Lenski 2000). Simulation results revealed at one site (POR8, an agricultural area in lowland Borneo) a more ‘clumped’ body size distribution than expected. This suggests common constraints on the size of the species group (Gotelli et al. 2003), which might also be an explanation for the generally small range in body sizes as well as the relatively uniform shape in Sphingids. Possibly predation by bats is an important mortality parameter for adult Sphingidae in flight (pers. obs.), which have mainly their flight speed and agility as a means of defence (Evans & Schmidt 1990). Giardini (1993) quantified the predation on adult Sphingidae in an urban environment in Italy and found that effects of bats were significant, although not as important as that of feral cats. Roosting sites of bats in West-Africa indicated that some species have a high preference for Sphingidae (K. Soer & J. Fahr, pers. com.). One might speculate, therefore, that the Sphingid-typical body shape, which enables the amazing flight abilities in this group, works only well and energy-efficient within a certain size range. Surprisingly, while biomechanical studies on hawkmoth flight are not rare (using mainly the North American *Manduca sexta* as a model organism, e.g. Wilkin & Williams 1993, Voigt & Winter 1999, Denny & Hale 2003, Wootoon et al. 2003), no studies were found that put the flight abilities of hawkmoths into an ecological context of predator escape. If evolution strongly restricts the radiation of Sphingid body sizes, because of bat predation or because of some other reason (e.g. hovering flight in front of flowers), it might be expected that ‘standard’ macroecological patterns regarding body size might be hidden in this taxon.

CHAPTER 6 - THE RANGE-ABUNDANCE RELATIONSHIP

Abstract

A positive interspecific relationship between the local abundance and the geographical distribution of species is so commonly reported that is appears as a ‘law’ of macroecology. However, the number of studies on this relationship is biased against invertebrates in tropical regions, hence opposing the global distribution in species richness. Here, a tropical moth family is used to explore the relationship, utilising range area measurements from GIS-supported distribution estimates and various types of local abundance measures, mostly based on light trapping.

A generally positive range-abundance relationship could be documented for the Sphingidae of Southeast-Asia. This is the first report of the relationship for tropical insects using comprehensive range measures and a sub-continental-wide extent of abundance measurements.

Abundance measurement appears as a crucial point in analysis: Regional means of local frequencies do not yield a range-abundance relationship, whereas correlations at local sites find significant effects. Meta-analysis of single-site correlations is suggested as a suitable method to circumvent the problem of habitat heterogeneity in abundance measurements.

Phylogenetic controls (independent contrasts) as well as partial range measures of Southeast-Asia-wide extent do not change results significantly. Apparently, there is an influence of geographical position, habitat disturbance and elevation on the strength of the relationship, whereas taxonomic affiliation (potentially linked to life-history and dispersal ability) as well as body sizes have no impact.

The *niche breadth hypothesis* tentatively receives the strongest support of the proposed mechanisms for a positive range-abundance relationship from the data: Range sizes are positively related to the number of utilised larval host plant families, whereas the correlation with mean local abundances is weak and does not hold with phylogenetically corrected data.

Introduction

A positive relationship between the local abundance and the geographical distribution of species has been documented in such an overwhelming number of studies (e.g. Bock & Ricklefs 1983, Bock 1987, Brown 1984, Gaston & Lawton 1988, Johnson 1998a, b, Frost et al. 2004, Lacy & Bock 1986, Murray et al. 1998, Pyron 1999, Blackburn et al. 1997, Quinn et al. 1997b, see also Gaston 1996a, Gaston et al. 2000 for further references and review) that it appears as a 'law' of macroecology (Colyvan & Ginzburg 2003). Not only its broad empirical support makes this relationship interesting, but also its potential to provide a link between various large-scale patterns of community organisation (Blackburn & Gaston 2001, Brown & Maurer 1989, Maurer 1999) such as species richness, relative abundance distributions or the distribution of ranges and body sizes. Furthermore, the *inter*specific range-abundance relationship is mirrored by an *intra*specific relationship of range and abundance in time series (e.g. Maurer 1999, Gaston et al. 1999a), and both variables are strongly linked to extinction (Gaston 1994b, Kunin & Gaston 1997, see also Jones et al. 2003, Keith et al. 2000, Purvis et al. 2000, Johnson 1998b, Alpizar-Jara et al. 2004).

However, considering the potentially pivotal role in the understanding of large-scale patterns in community assemblage and its consequences for applied purposes such as conservation and harvesting (see e.g. Gaston et al. 2000, Warren et al. 2003, Luck et al. 2004, Jennings & Blanchard 2004, Hoffmann & Welk 1999), research on the range-abundance relationship still has a number of shortcomings that might be broadly placed in three categories:

1) Despite a broad taxonomic breadth of investigations (see e.g. references in Gaston et al. 2000), there is a *taxonomic and geographical bias* towards studies on vertebrates and plants in temperate regions (Maurer 1999, Gaston 1996a). Particularly tropical invertebrates are only rarely addressed in studies of range-abundance distributions (but see e.g. Hanski 1982, Hanski et al. 1993, Gazhoul 2002). This is directly opposing the global distribution patterns of biodiversity, which is concentrated among the invertebrates of tropical regions, particularly the herbivorous insects (see e.g. Myers et al. 2000, Godfray et al. 1999, Pimm & Brown 2004, Rosenzweig 1995). Thus, confirmations of the relationship in tropical insects are urgently needed to justify the assumption of a generally positive range-abundance distribution (Gaston 1996a), although so far few general deviations from the 'classical' macroecological patterns of temperate birds (e.g. Brown 1984) were found (Brown 1999).

2) There are *inconsistencies in the measurement* of the investigated parameters across different studies. Particularly the scale and resolution of the range area measurement differs greatly between studies (e.g. Gaston 1996a), from the total, *comprehensive* ranges of the investigated assemblage to small, *partial* fractions of their actual range. In most cases this is caused by a lack of data on comprehensive ranges of many groups, such as tropical invertebrates. Analyses on different scales of measurement might actually measure different phenomena (Blackburn & Gaston 1998, Gaston 1996a, see also Hartley 1998), whereas the range-abundance relationship becomes trivial at a very small scale (e.g. Stoffels et al. 2003). Despite an overall good correlation of the extent and resolution of range measurements (e.g. Quinn et al. 1996, Blackburn et al. 2004, Brändle et al. 2002a, see also chapter 4.2) there appears to be a trend towards stronger range-abundance relationships for *partial* (vs. *comprehensive*) measures, and for measures of *area of occupancy* (i.e., the number of grid

cells where a species is present) vs. the *extent of occurrence* (i.e., the outermost records of a species' distribution; see Gaston 1996a for terminology). The measurement of local abundance is also not as trivial as it first appears: Means of a species' abundance across the sites where it occurs are often applied as an abundance measure (as means over all sites would produce a bias, see Lacy & Bock 1986), although in all but the few cases of spatially extensive, yet fine-scaled counts (such as e.g. for British birds, BirdLife International/European Bird Census 2000) this measure relies on the assumption of fairly uniform spatial abundance distributions of species, whereas in reality such distributions are often complex and multi-peaked (Hengeveld 1990, Gaston et al. 1997, Brewer & Gaston 2003) due to habitat heterogeneity (see e.g. Schoener 1987). Adding to such spatial heterogeneity, populations might be fluctuating considerably on a temporal axis, both randomly or directed, and with taxon-specific constraints (Gaston & Blackburn 2002, Maurer 1999, Lawton 2000, see Selas et al. 2004, Bjørnstad et al. 1998 for examples of moths). The amplitude of such fluctuations has been found to be connected to range size (e.g. Glazier 1986, Bowers 1988) or mean abundance (Kunin & Gaston 1997), and mean abundance measures appear to be negatively related to the census area (in British birds: Gaston et al. 1999b). As an alternative to mean abundance the maximum local abundance of a species (temporally and spatially) has been used (e.g. Quinn et al. 1997b), which might be a suitable measurement of a species' *potential* frequency under favourable habitat conditions.

3) For a satisfying acceptance of a hypothesis it must be causally embedded in previously established knowledge (e.g. Maurer 2000). A number of biological causalities as well as artefacts of sampling and phylogeny have been proposed to be responsible for positive range-abundance relationships (e.g. Gaston et al. 1997, 2000, McGill & Collins 2003, Hubbell 2001), which all succeed in an explanation for the observed patterns – but often fail to be rigorously testable on realistic data sets as they are not mutually exclusive. As an experimental approach to the topic at natural spatial scales is impossible or unethical in most life-size ecosystems (but see e.g. Holt et al. 2004, Warren & Gaston 1997, Lawton 1998), only a more detailed analysis of the natural variability in the pattern remains as a means to provide further information for hypothesis generation and -testing. This variability might involve, for example, differences between taxa, life styles, habitats, regions or evolutionary age of taxa, which might lead to positive, non-significant, or negative relationships (e.g. Johnson 1998b, Gaston & Lawton 1990, Arita et al. 1990). Alternatively, a closer analysis of the shapes of different range-abundance relationships might yield further hints on the mechanisms that created them (e.g. Hartley 1998, but see Gaston et al. 1998).

A spatially extensive analysis of the range-abundance relationship of Southeast-Asian hawkmoths is presented here. Besides butterflies, this Lepidoptera family is probably the best known of the tropical insect taxa (e.g. Kitching & Cadiou 2000), which gives the possibility to further diminish the above mentioned taxonomic and geographical biases. A dichotomy in patterns of biogeography, larval host plant use, and local biodiversity (such as reaction to habitat disturbance: see previous chapters, Holloway 1987a, Schulze 2000) was shown between the subfamily Smerinthinae on the one hand, and the subfamilies Sphinginae and Macroglossinae on the other hand, and it has been tentatively suggested (see previous chapters, Schulze 2000) that these could be caused by life-history differences related to adult feeding (see e.g. Lemaire & Minet 1998, Tammaru & Haukioja 1996). It may thus be expected that the different taxa also show different range-abundance relationships. Results based on different measures of local abundance and on different scales of range measurements are compared. Furthermore, meta-analysis (Scheiner & Gurevitch 2001) is introduced as a novel, yet powerful tool of range-abundance analyses. This method, which is commonly used to re-analyse published results from different studies on the same topic (see references in Rosenberg et al. 2000, examples in ecology are Gurevitch et al. 2000, 1992, Hillebrand et al. 2001, Hyatt et al. 2003, Levine et al. 2004), does not only allow to overcome some of the problems of local abundance measurements (see above) by analysing correlations on a site-by-site basis, but also gives the option of exploring differences in the strength and direction of correlations depending on region or habitat, e.g. by filtering cases with and without positive relationships.

Methods

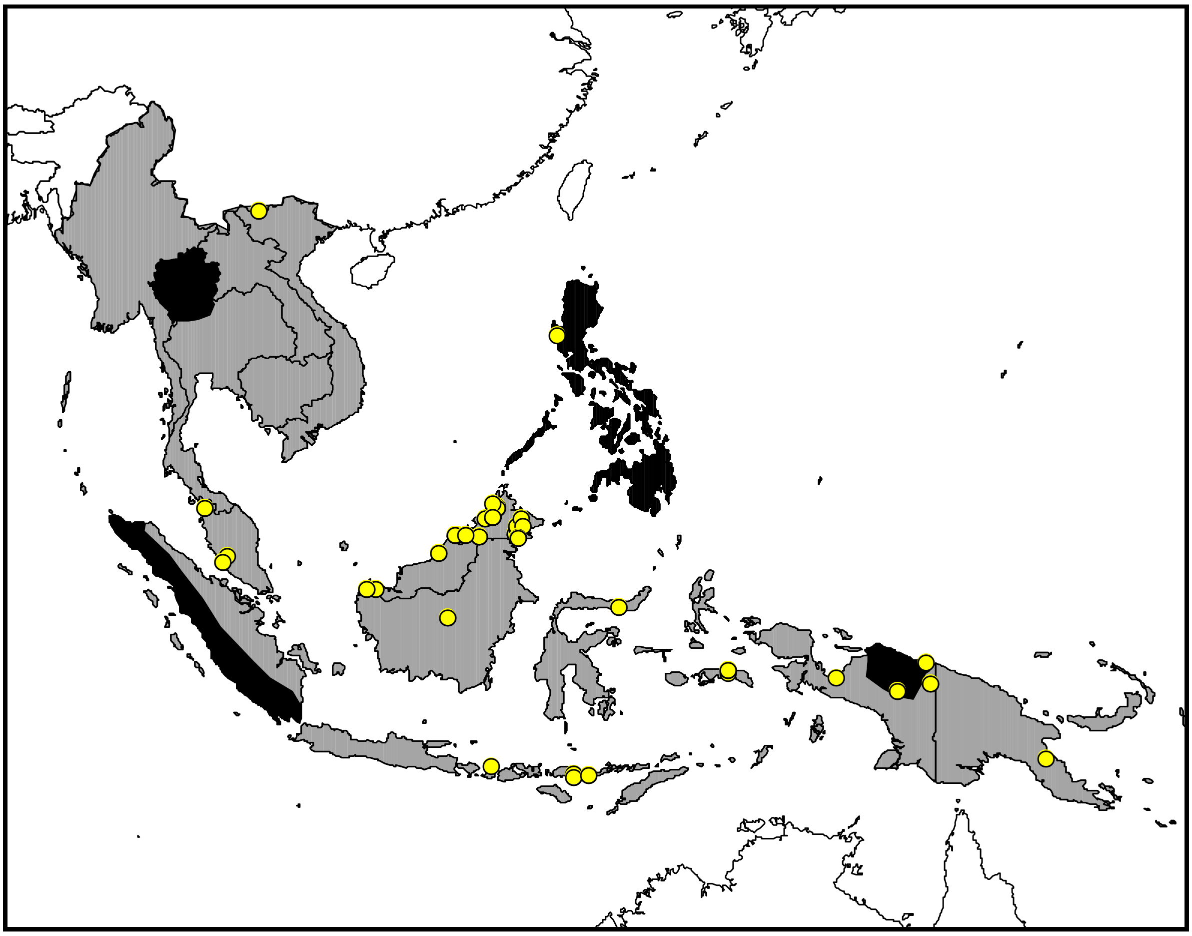
Data sources

1) Geographical range of species

The geographical ranges of hawkmoth species were estimated in a GIS-supported procedure that is described and discussed in more detail in Beck & Kitching (2004) and in the chapters 1.3 & 4.1. Range areas were calculated (Hooge et al. 1999), which are hereafter used as a measure of range size. Other measures of range size, such as minimum convex polygons or latitudinal and longitudinal extent correlate well with range area (see chapter 4.2). In order to explore scale effects of range measurements, those parts of the global (*comprehensive*) range estimates which fall into Southeast-Asia (as defined in Beck & Kitching 2004) were cut out and used as *partial*, subcontinent-wide range estimates. Thus, they might contain only a part of the global range of a species, but their geographical *resolution* is equal to that of the *comprehensive* measurements (see chapter 4.2 for correlations between *comprehensive* and various *partial* range measures).

2) Assessments of local abundance

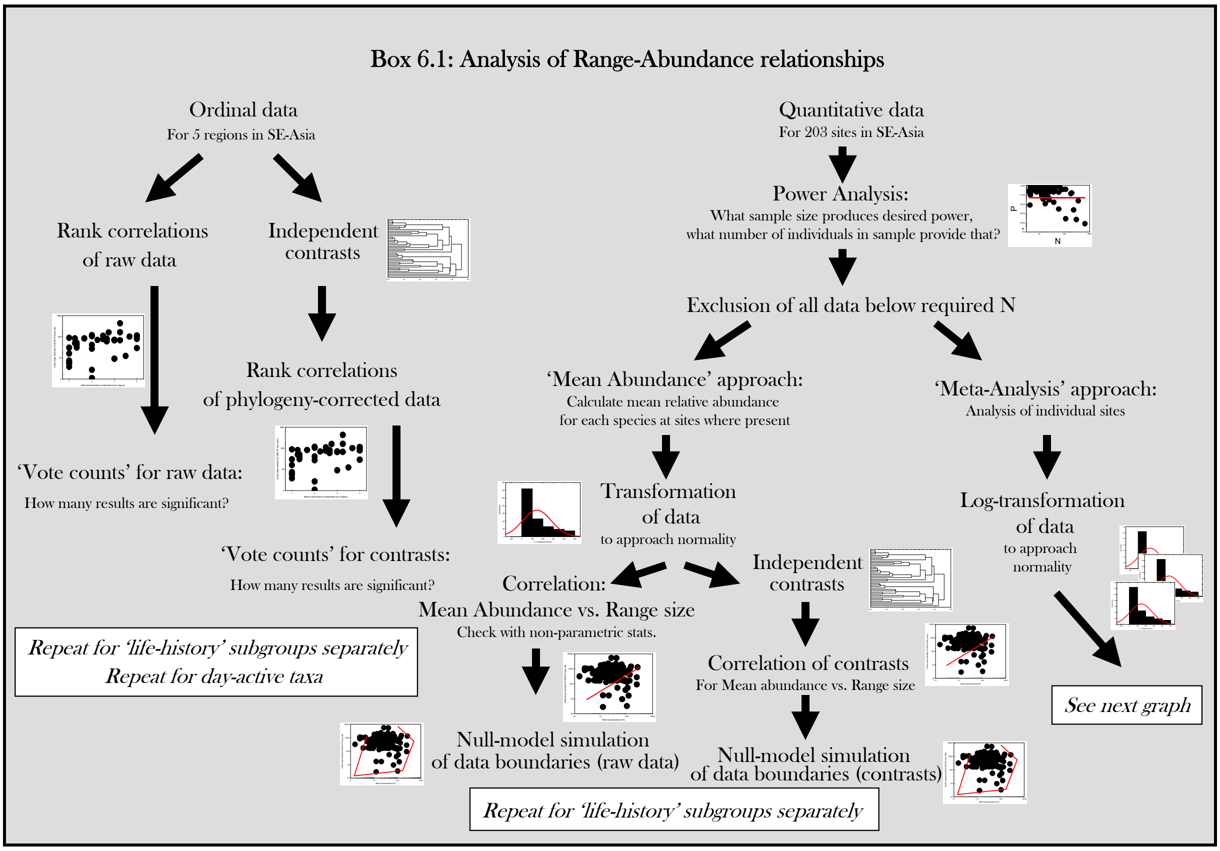
Ordinal assessments of local abundance or commonness are published for Sumatra (Diehl 1982) and the Philippines (Treadaway 2000). Several collectors in other regions of Southeast-Asia were asked to assess the commonness of species in their collection or experience in a similar fashion on a four-point scale (1=‘very rare’ (usually one of few specimens in collection), 2=‘rare’, 3=‘uncommon’, 4=‘common’; the latter two categories usually referred to species which hobby-collectors would not quantitatively take). Such ordinal data were retrieved for Thailand (mainly north-western part, Ian. J .Kitching pers. com.), Peninsular Malaysia (Genting Tea Plantation, Henry Barlow pers. com.) and New Guinea (northern Indonesian Papua, mainly Jayapura and Cyclops mountains, Henk v. Mastrigt pers. com.; see map 6.1). While these data are less precise than quantitative samples (see below) and might suffer from different use of the ‘commonness’-scale by different persons (as a consequence data were not pooled), they result from considerably longer experience with the local

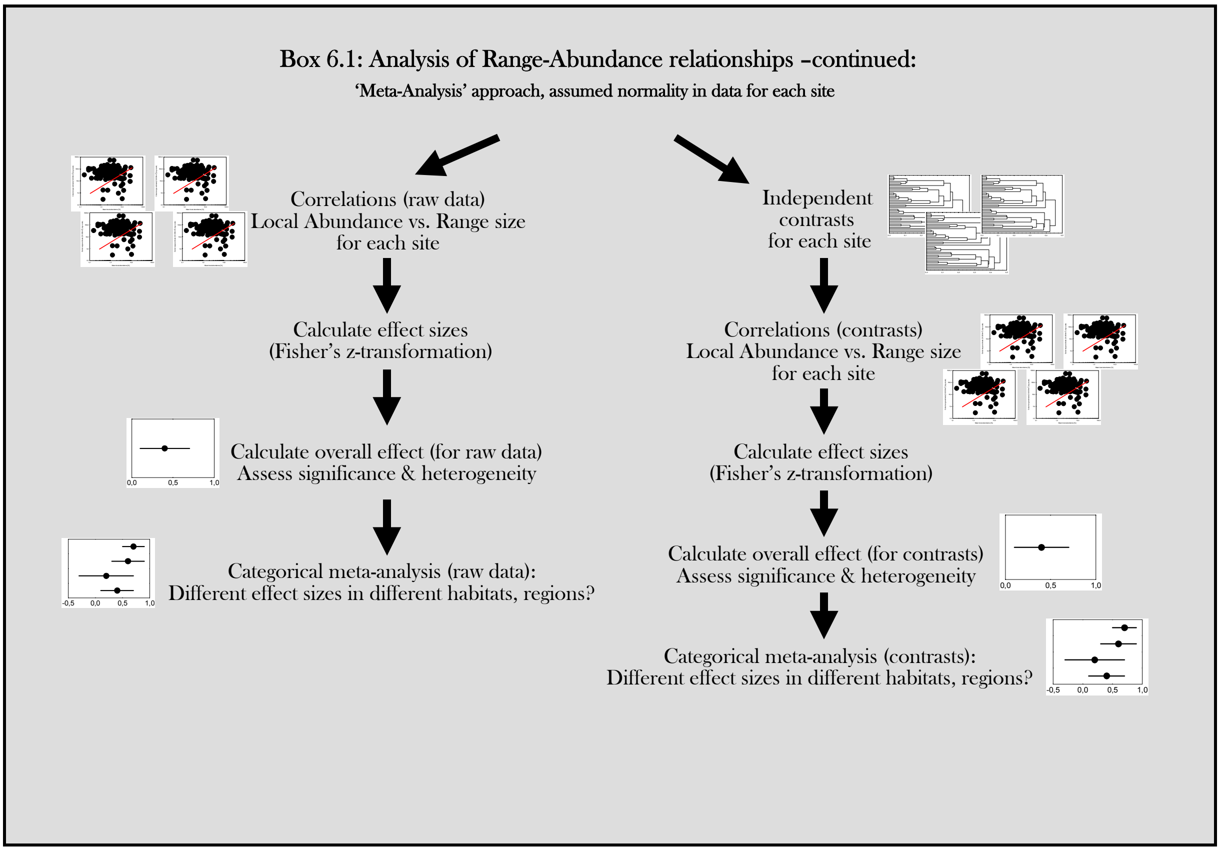


Map 6.1 shows the locations of quantitative sampling sites with ≥13 species and/or ≥50 specimens as well as the approximate extent of sampling regions (black shaded) from which ordinal abundance estimates were available. The ordinal data from Peninsular Malaysia stem from a single sample site in the Genting highlands (see text for details and data sources). Note that some sites are so close to each other that they appear as one point on the map.

abundance of Sphingid species in the region (several decades of sampling in some cases), which might filter out untypical temporal highs or lows in population densities of species that would be used indiscriminately in quantitative, short-term collection data. Furthermore, these abundance estimates contain some extremely rare species that would probably not be found at all in short-term sampling (i.e., singletons or doubletons in >25 years of collecting). Additionally, four of the five sources also provided abundance estimates for day-active taxa of hawkmoths which require other methods of sampling than light-trapping (i.e. net-catches at flowers, etc.), and for which no quantitative data were available at all.

Quantitative light trapping data of hawkmoth abundance were compiled from published sources (Chey 1994, 2002a, Holloway 1976, Schulze 2000, Tennent 1991, Zaidi & Chong 1995), unpublished collections (collected or curated by Jeremy D. Holloway, Wolfram Mey, Ulf Buchsbaum, Azmi Mahyudin, Geoff Martin; Vietnam-data from an unknown source was mediated by Torben Larsen) and own field work in Borneo, Peninsular Malaysia, the Lesser Sunda Islands and New Guinea. Northern Borneo is by far the best covered region for quantitative data. Local sample sizes vary greatly and were filtered for analysis accordingly (see below; 113 sites have data for less than 20 specimens, while six sites provide data for more than 600 specimens). Map 6.1 shows the location of all those sites that were actually used for analyses of the range-abundance relation. All quantitative data stem from nightly light trapping. However, only own sampling (see appendix I) applied a standardised method of several consecutive nights of all-night hand-sampling at 45 Watt blacklight tubes (on the


Box 6.1: Analysis of Range-Abundance relationships


Box 6.1: Analysis of Range-Abundance relationships –continued:

'Meta-Analysis' approach, assumed normality in data for each site

Lesser Sunda Islands) or a 125 Watt Mercury-Vapour lamp (elsewhere). Taxa that are known to be day-active were generally excluded from analysis in the few cases when they appeared at light (assuming they represent only chance-catches of specimen which rested in nearby vegetation and were then attracted to the light source).

Methods of analysis

A thorough analysis of the range-abundance correlations, acknowledging for different types of data, phylogenetic autocorrelation, different types of range measurement, and searching for effects of taxonomy, region and habitat, requires a complex assembly of analyses which is schematically displayed in box 6.1, and explained in more detail below.

Phylogenetic effects

Correlations (as well as other statistics) of species' characters were criticised as they may give misleading results in comparative studies due to the statistical non-independence of species that share a common phylogeny (Harvey & Pagel 1991, Garland et al. 1999). Using a randomization test (Abouheif 1999, Reefe & Abouheif 2003), it was shown that range sizes (p=0,010, chapter 4.2) as well as mean local frequencies (p=0,035, chapter 3.2) are phylogenetically autocorrelated (results for raw data; transformed data, which were used for correlation analyses (see below) do not show a significant phylogenetic signal, but trends for it). Independent contrasts (Felsenstein 1985) are the most commonly employed technique of phylogentic correction (Harvey & Pagel 1991, see also Garland et al. 1999, Garland & Ives 2000). Contrasts were calculated using the systematics in Kitching & Cadiou 2000 and some unpublished updates (I.J. Kitching pers. com.) as a substitute for a phylogeny. Contrasts were calculated with the computer program *Phylip 3.61* (Felsenstein 2004; all branch lengths were set to 1 except at unresolved nodes, which were set to 0,0001).

1) Ordinal data

Spearman rank correlations were used to assess the relation between global range area and local abundance estimates in five regions of Southeast-Asia. Differences between taxonomic groups among the Sphingidae were explored by separate correlations for Smerinthinae, Macroglossinae and Sphinginae. Rank correlations of day-active taxa were calculated separately for the regions if data were available, but no independent contrasts were calculated for this data as they consist of a maximum of five genera in one region (Thailand, much less in other regions) with most species of the genus *Macroglossum*, for which no intra-genus phylogeny was available. To explore the effects of different range measurements on the judgement of range-abundance relationships, correlations for night-active taxa were re-calculated (including independent contrasts) for *partial*, Southeast-Asia-wide range areas.

2) Quantitative data

Sample size considerations

Power, or the probability of a Type II-error (i.e., the false acceptance of the null hypothesis), is of essential concern to ecological field studies where data replication is usually attained only with great effort. This applies even more to comparative studies, where not specimens but species are the unit of ‘sample size’. Although power does not act directly on the results of meta-analysis or an analysis of pooled data (see below), it was desirable to exclude data from samples which were so small that mainly random effects must be expected, as these data would only inflate uncertainty and error rates while not adding much information. Preliminary analyses of the present data set have shown a strong dependency of results on the exclusion of small sample sizes. To assess limits for the inclusion of sampling sites in the analyses, correlations between the twelve sites with the largest number of species (30-67) were calculated to estimate what effect sizes (Pearson’s r) have to be expected, if such correlations exist. Six correlations were significant ($p<0{,}05$, most $p<0{,}01$) and had a median effect size of $r=0{,}44$ (min. 0,37, max. 0,47). *A priori* power analysis (*GPower 2.0*, Faul & Erdfelder 1992) revealed that a minimum sample size of 13 species is necessary to find an effect of that magnitude with a Type I-error of $p=0{,}05$ and a minimum required power of 0,50. For comparison, an ‘ideal’ data analysis which keeps both (Type I & II) error probabilities <0,05 (i.e., power >0,95) would require a sample size of 47 species, which were found only at two sampling sites.

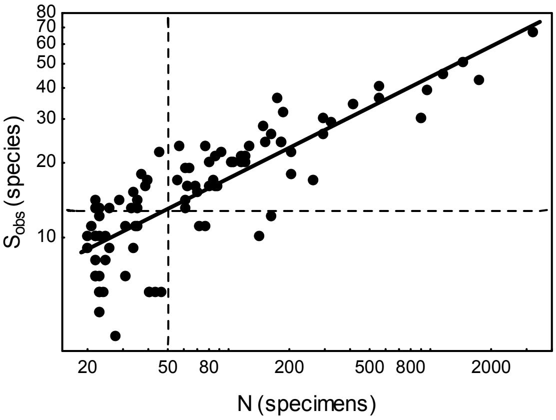


Figure 6.1 shows the relationship between specimens and species at 93 sampling sites (log-scale, only sites with N≥20). Dashed lines show the limits of inclusion to analyses (see text) as a consequence of power analysis.

As a consequence, only sites with more than twelve species were included in analyses on site-by-site basis. For analysis based on mean frequencies (as percent-abundance, see also below) this is not a relevant limit, but a restriction to larger sample sizes was also desirable as small samples might bias means due to a low resolution of the relative abundance measurement. A species number of 13 translates to a specimens number of approximately 50 (see figure 6.1), which was used as an inclusion limit of sampling sites for mean frequency analysis in order to keep consistency in the analyses. This implies that the resolution of relative species frequencies is two percent. The geographical positions of all sampling size with at least 13 species or at least 50 specimens are displayed in map 6.1.

Transformations and normality of data

Relevant data are not normally distributed, but highly right-skewed (i.e., small ranges or frequencies are the most commonly encountered data). Local abundance data follow a log-normal distribution (see chapter 3.2) and were consequently log-transformed for single-site analyses (see below). However, for a meaningful calculation of mean abundance, data had to be converted to relative abundances first (see below). These relative abundances could be normalised by an *arcsinus-square root* transformation (Southwood & Henderson 2000) at all sites. Range area data show a considerable 'normalisation' after log-transformation, but still contain a left-skew which leads to rejection of a normal distribution for pooled data (KS-test, p<0,01; chapter 4.2). As parametric statistics were desirable for a measurement of effect sizes (see below), log-transformations were applied to all range area data in order to attain 'almost-normality' – no significant deviations (KS-tests, p<0,05) from normality were observed for transformed range data for single sampling sites due to reduced sample sizes.

Mean frequencies

Light trapping does not allow a measurement of absolute abundances or densities in a habitat, as habitat-independent factors (such as weather, moonlight, Yela & Holyoak 1997) influence the activity of moths or the attractivity of the light, or both. However, light trapping data are probably a good indicator of the *relative abundance* (or frequency) of species in a habitat, if species which do generally not come to light are excluded from analyses (see chapter 2). The local abundance of species *i* was converted into a frequency as $F_i = Abu_i / \Sigma Abu_{all\ spec}$. Means were calculated after appropriate transformation of frequencies (see above), as the use of raw frequencies was not feasible due to large deviations from normality of species' frequencies over the sampling regions, which is probably a consequence of habitat heterogeneity.

Null-model simulation

Macroecological relationships are often not appropriately described by linear relationships (Gotelli 2001), but rather fill a non-random section of a graph. Particularly the range-abundance relationship has been described as triangular (see e.g. Gaston et al. 2000) rather than linear. To explore such patterns null model simulations (see e.g. Gotelli 2001, using the computer program *EcoSim 7.58*, Gotelli et al. 2003) were used to assess the probability that observed patterns could be generated by chance. Data for two variables were randomised 10.000 times (data defined constraints, asymmetric data distributions) and compared to original data, testing for 1) triangle relationships, 2) the slope of a linear regression, 3) *a priori* expected data boundaries in the upper left and lower right corner of the graph (see e.g. figure 6.4).

Meta-analysis on site-by-site basis

Product-moment correlations were calculated between (log-transformed) range areas and local abundances for each site in analysis. Using the sample sizes (number of species) and correlation coefficients (Pearson's r), Fisher's z_r and their variance were calculated as adequate effect size measures for meta-analysis (using *MetaWin 2.0*, Rosenberg et al. 2000). A fixed-effects model was used to assess the overall effect size and its confidence intervals. An effect size which is significantly different from zero indicates an overall valid relationship.

Furthermore, continuous and categorical models were used to explore effects of various habitat parameters on effect sizes.

Results

1) Ordinal data

a) Night-active taxa

Despite the crude measurement of local commonness, four regions display a positive rank correlation between local abundance and comprehensive range size, whereas data from

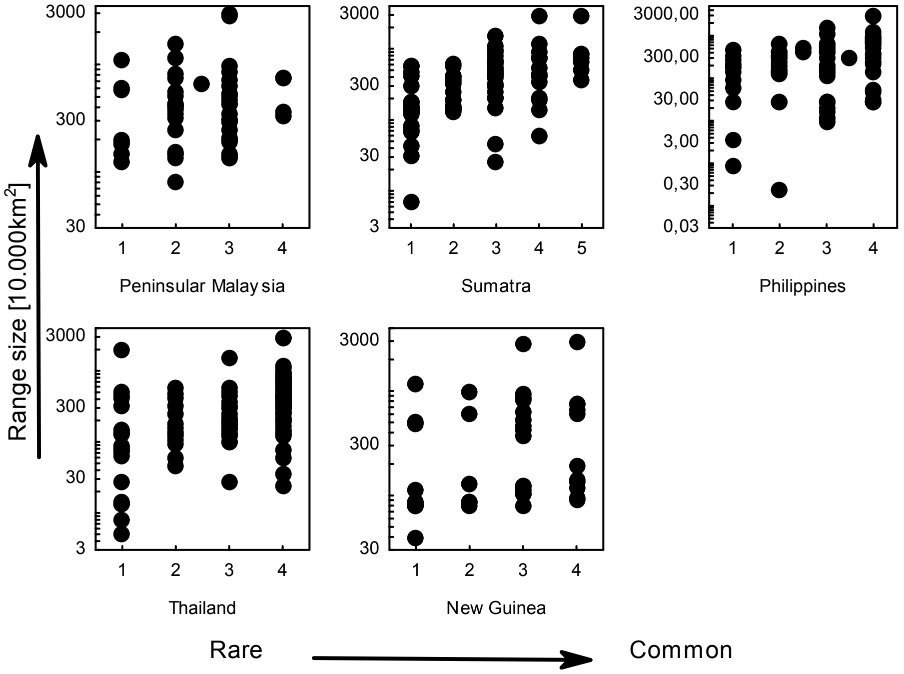


Figure 6.2a: Relationships between comprehensive range and ordinal abundance estimates in five regions for night-active, light-attracted taxa of Southeast-Asian Sphingidae.

	Raw data			*Contrasts*	
comprehensive	**Species**	**Spearman's R**	**p**	**Spearman's R**	**p**
Thailand	*127*	0,530	<0,0001	0,367	<0,0001
Pen. Malaysia	59	0,125	0,347	-0,084	0,532
Sumatra	*91*	0,567	<0,0001	0,447	<0,0001
Philippines	*89*	0,327	0,002	0,321	0,004
New Guinea	46	0,455	0,001	0,215	0,187
No. of sign. correlations			*4*		*3*
partial					
Thailand	127	0,604	<0,0001	0,478	<0,0001
Pen. Malaysia	59	0,277	0,034	0,076	0,568
Sumatra	91	0,614	<0,0001	0,490	<0,0001
Philippines	89	0,387	<0,001	0,322	0,004
New Guinea	46	0,450	0,002	0,238	0,144
No. of sign. correlations			*5*		*3*

Table 6.1: Spearman rank correlations of *comprehensive* (above) and *partial* (below) range and ordinal estimated commonness in five regions, for raw data and independent contrasts (Felsenstein 1985, 2003).

Peninsular Malaysia do not show any significant relationship (figure 6.2a, correlation data in table 6.1). Furthermore, three of the four significant correlations persist after controlling for effects of phylogeny (table 6.1), while data from New Guinea loose their relationship if independent contrasts are used instead of raw data.

In order to explore the influence of taxonomical affiliation on the relationship, the Smerinthinae and the two other subfamilies (Macroglossinae, Sphinginae) were tested separately for correlations. Results are presented in table 6.2: Macroglossinae and Sphinginae exhibit significant positive relationships in four regions (data were pooled as both subfamilies showed the same trends in preliminary tests). In the Smerinthinae only two regions show a significant positive relationship, and ‘borderline’ significant positive trend (p=0,05) was found in yet another region.

	Macroglossinae & Sphinginae			*Smerinthinae*		
	Species	**Spearman's R**	**p**	**Species**	**Spearman's R**	**p**
Thailand	76	0,529	<0,0001	51	0,510	<0,001
Pen. Malaysia	43	0,158	0,311	16	0,261	0,329
Sumatra	62	0,632	<0,0001	29	0,312	0,010
Philippines	61	0,501	<0,0001	28	-0,158	0,422
New Guinea	41	0,431	0,005	5	0,872	0,054
No. of sign. correlations			**4**			**2**

Table 6.2: Spearman rank correlations of *comprehensive* ranges and ordinal estimated commonness in five regions (raw data only), divided by subfamilies (Macroglossinae & Sphinginae were pooled as they follow very similar trends).

b) Day-active taxa

Range-abundance correlations appear weaker in day-active taxa than in night-active groups and are non-significant in three of four regions (table 6.3). However, all relationships are positive at Spearman’s R >0,25. Therefore, non-significance might at least partly be a consequence of low sample sizes (i.e., number of species). Data for four regions are displayed in figure 6.2b.

c) Partial range measures

In order to assess the influence of scale some of the analyses were repeated using partial ranges rather than global, comprehensive ranges as above. Table 6.1 shows results for night

		Comprehensive range		*Partial range*	
	Species	**Spearman's R**	**p**	**Spearman's R**	**p**
Thailand	30	0,272	0,146	0,405	0,026
Pen. Malaysia	13	0,376	0,205	0,677	0,011
Sumatra	23	0,315	0,144	0,317	0,141
Philippines	32	0,478	0,006	0,507	0,003
No. of sign. correlations			*1*		*3*

Table 6.3: Spearman rank correlations of range area and ordinal estimated commonness of day-active Sphingidae taxa in four regions (raw data only).

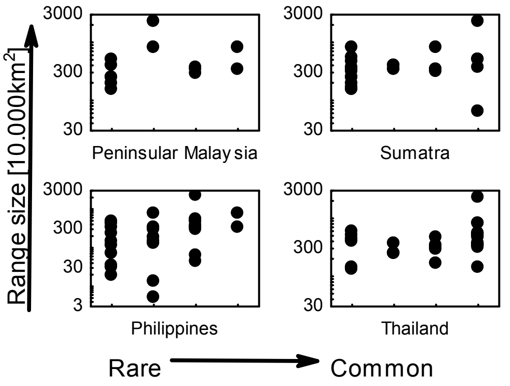


Figure 6.2b: Relationship between comprehensive range and ordinal abundance estimates in five regions for day-active taxa (genera *Sataspes, Cephonodes & Macroglossum*) of the Southeast-Asian Sphingidae. See table 6.3 for statistical testing.

active taxa. In comparison to comprehensive measures, correlations are generally stronger (comprehensive range: Spearman's $R_{mean±SD}$=0,401±0,179, partial range: $R_{mean±SD}$=0,466±0,144; for contrasts, comprehensive range: $R_{mean±SD}$=0,253±0,206, partial range: $R_{mean±SD}$=0,321±0,173). For day-active taxa, the difference is even more evident (table 6.3): Three out of four correlations are significant if the partial range concept is applied. Similar to night-active taxa, Spearman's R are higher than for comprehensive range measurements (comprehensive range: $R_{mean±SD}$=0,360±0,089, partial range: $R_{mean±SD}$=0,467±0,155).

2) Quantitative data: mean frequencies

Linear regressions of the mean frequency of species and their range size are not significant (table 6.4) and appear to be negative (see figure 6.4). As range data are not normally distributed despite log-transformations (see methods), non-parametric tests (Spearman rank correlations) were also used to check data for deviating results. Interestingly, they indicate a trend ($p<0,10$) for a *positive* relationship for comprehensive ranges (raw data & contrasts), which indicates a strange data structure for mean abundances (see discussion). Rank statistics of medians of non-transformed frequencies data also indicate positive relationships, although a plot of data is reminiscent of figure 6.4 (not shown).

	N	**r^2**	**p**
Range – mean frequency	132	0,006	0,385
Contrasts	131	0,029	0,051
Partial range – mean frequ.	132	0,006	0,381
Contrasts	131	0,001	0,797

Table 6.4 shows results of Pearson product-moment correlations of mean frequency and range area for Southeast-Asian hawkmoths. All relationships are (non-significantly) negative.

Null model simulation suggests that raw data have a non-random data boundary in the upper left corner (i.e., there are no locally rare species with large ranges; see figure 6.4 for data boundaries) and a strong trend

	Comprehensive range		*Partial range*	
$p_{(obs≠sim)}$	**Raw data**	**Contrasts**	**Raw data**	**Contrasts**
Triangle-shape	0,046	0,355	0,527	0,220
Regression slope	0,188	0,030	0,190	0,396
Lower right boundary	0,054	0,004	0,066	0,005
Upper left boundary	0,012	0,605	<0,0001	0,139

Table 6.5: Results from *Range-Mean Frequency* null-model simulations (10.000 randomisations, asymmetric boundaries), for *comprehensive* and *partial* (SE-Asia wide) range estimates. Transformed data were used to allow direct comparison to regression results. Non-transformed raw data did not yield qualitatively different results.

for a boundary in the lower right corner (i.e., most locally common species have a large range). Independent contrast analysis confirms the lower right boundary, while the upper left boundary disappears.

Partial (Southeast-Asia-wide) range areas (tables 6.6, 6.7) qualitatively yield the same results as comprehensive range measures. Null model analysis (table 6.5) revealed a data boundary in the lower right corner (i.e., there are no locally common but geographically restricted species).

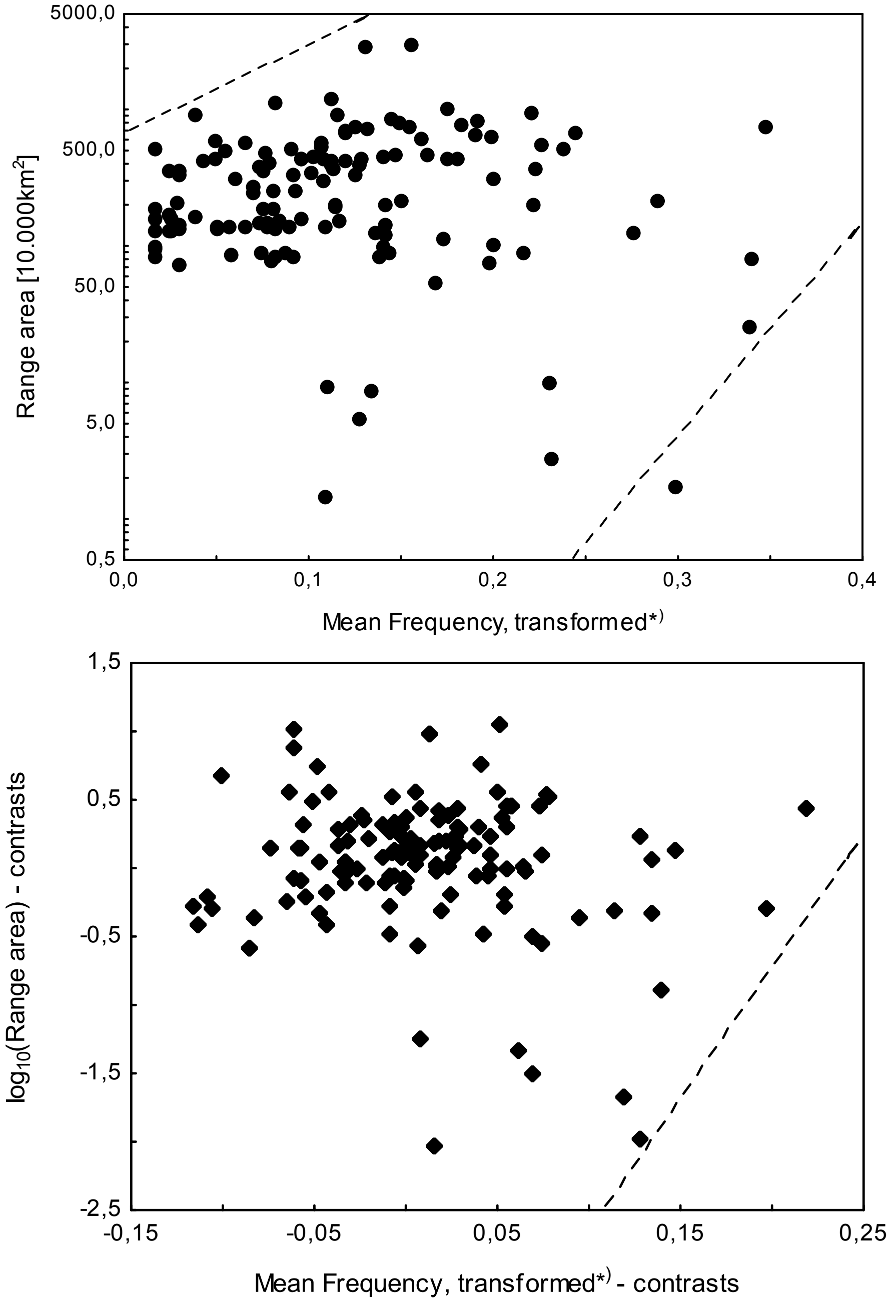


Figure 6.4: Correlations of mean local frequency and comprehensive range for 132 hawkmoth species. Data boundaries from null-model simulation (see text) are shown as dashed lines (schematic examples only). The upper graph shows raw data, the lower graph independent contrasts. *) Frequencies were *arcsinus-square root* transformed to attain a normal distribution prior to mean calculation, see methods.

A taxonomic split of data into Smerinthinae and the two other subfamilies (only raw data, table 6.6) indicated no differences in linear regression analyses (both non-significantly negative), whereas null-model analysis showed a (non-significant) trend towards an upper left boundary only in Macroglossinae and Sphinginae (i.e., locally rare species do not have large ranges).

	Correlation analysis			*Null model simulation*, $p_{(obs \neq sim)}$			
	N	**R**	**p**	**Triangle shape**	**Regr. slope**	**Upper left boundary**	**Lower right boundary**
Macroglossinae & Sphinginae	81	-0,135	0,229	<0,001	0,204	0,061	0,004
Smerinthinae	51	-0,194	0,172	0,016	0,291	0,306	0,002

Table 6.6 shows results of correlation analyses (Pearson product moment) and null-model simulations (10.000 randomisations) for the two life-history groups in the Sphingidae. Only raw data, no independent contrasts, were used in this analysis.

The maximum frequency of a species might also be used for the investigation of the range-abundance relationship (e.g. Quinn et al. 1997b). Using the same data set and transformations, no new insights are gained if compared to mean frequency measures: Maximum frequencies do not correlate with range size (N=132, Spearman's R=-0,068, p=0,441; data are not normally distributed), nor do null model simulations reveal any significant data boundaries if compared to simulated data. Furthermore, mean frequencies and maximum frequencies are not correlated (N=132, Spearman's R=0,091, p=0,300), while such correlations were reported for abundance in other data sets (e.g. McGill & Collins 2003).

3) Quantitative data: meta-analysis of site-by-site correlations

Eight of 58 local range-abundance correlations (figure 6.5) are significant at p<0,05 for raw data, nine of the correlations are significant for independent contrasts. However, contrary to this apparently low 'vote count', a summary of effect sizes (z_r) shows a clear and significantly positive effect (raw data: z_r=0,179, 99 percent confidence intervals from bootstrap: 0,086-0,269; independent contrasts: z_r=0,158, 99%CI_{boot}: 0,042-0,245). Effect sizes were analysed for their total heterogeneity Q_T (see Rosenberg et al. 2000), testing the null hypothesis that variability of effect sizes is solely due to sampling error. For raw data, effect sizes indicate a trend to higher than random heterogeneity ($Q_{T(df=57)}$=68,4, p=0,143), which becomes highly significant for independent contrast data ($Q_{T(df=57)}$=85,2, p<0,01). Thus, it is justified and necessary to explore effect size data for differences between groups of sample sites, such as regions, habitat disturbance (in three classes: primary forest, secondary forests, and open, heavily disturbed habitats; see also chapter 3.1) and elevation.

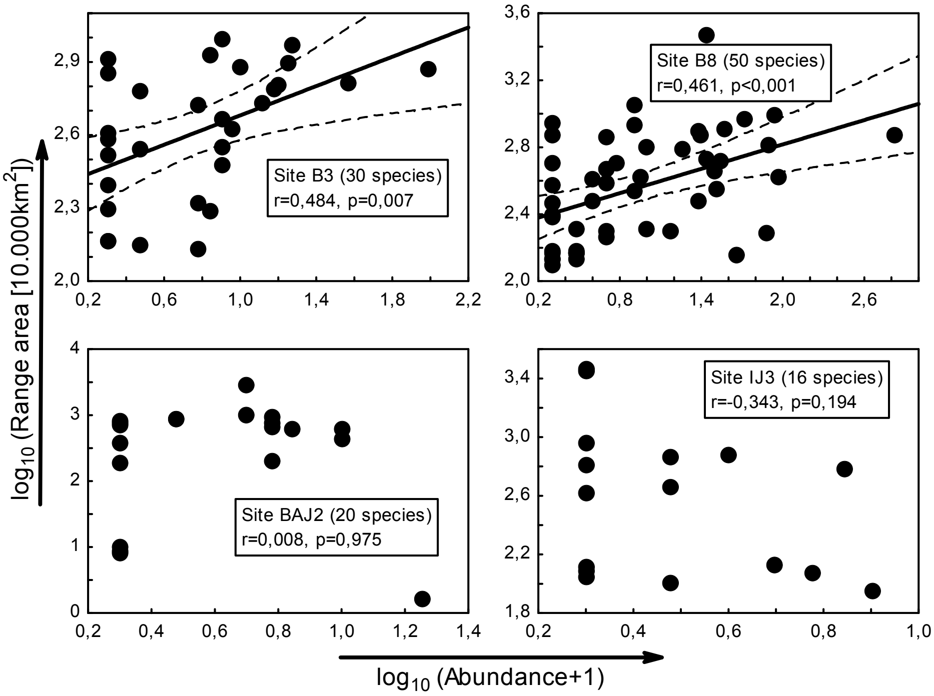


Figure 6.5 shows some examples of *local abundance – range area* plots for single sites. The upper two graphs show two significantly positive relationships (both from Borneo), the lower graphs show non-significantly positive (left, from Flores) and negative (right, from New Guinea) relations. 58 such correlations were calculated for meta-analysis.

Figure 6.6 shows effect sizes separately for regions. Differences between effect sizes are not significant (see 95 percent confidence intervals), but strongly suggest a geographical gradient from the West to the East of the archipelago: West of 'Webers's line' (between Sulawesi and the Moluccas, e.g. Monk et al. 1997) all regional effect sizes are significantly greater than zero, while East of there none of those regions which permitted the calculation of confidence intervals show a significant positive effect.

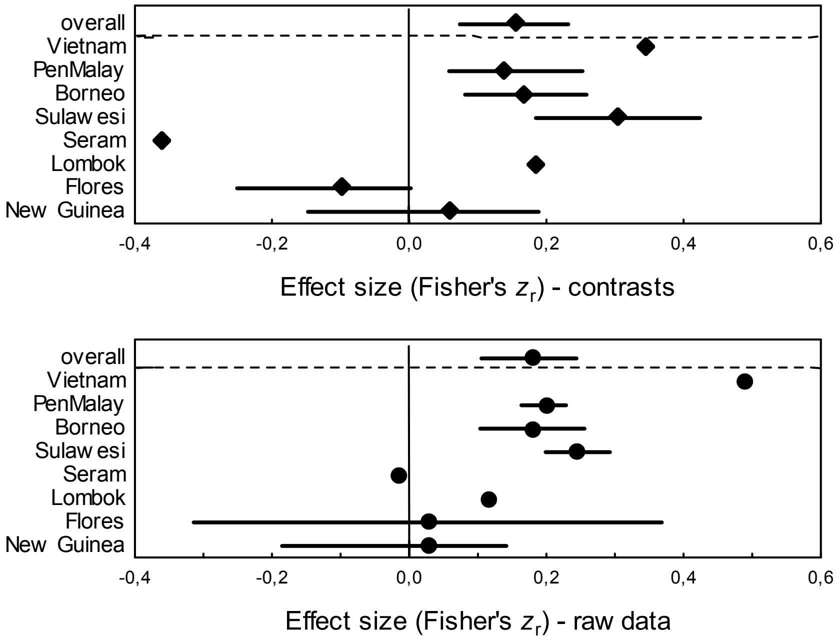


Figure 6.6: Average effect sizes and 95% confidence intervals (bootstrap) as a result of a categorical meta-analysis for range-abundance relationships at 58 sites from different regions/islands. The numbers of sites in each region are 1 (in Vietnam), 2 (Peninsular Malaysia), 43 (Borneo), 2 (Sulawesi), 1 (Seram), 1 (Lombok), 3 (Flores) and 5 (New Guinea).

Similarly, only in primary forests an overall significantly positive effect can be found, while secondary forests and open, heavily disturbed sites have effect sizes which are not significantly greater than zero, but also not significantly smaller than the effect size of primary forests (figure 6.7). A continuous meta-analytic model by site elevation shows a very weak negative regression of effect sizes with altitude (N=53, slope =-0,0001) which is non-significant for raw data ($p_{rand}>0,20$), but becomes a trend ($p_{rand}<0,10$) if contrasts are considered. Besides this, no qualitative distinction between analyses of raw data and independent contrasts were observed.

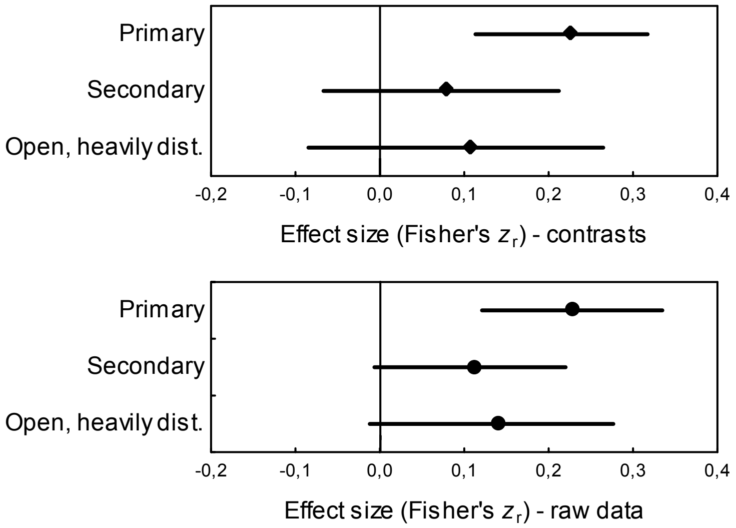


Figure 6.7: Average effect sizes and 95% confidence intervals (bootstrap) as a result of a categorical meta-analysis for range-abundance relationships from sites with different degrees of (mostly anthropogenic) disturbance. The numbers of sites in each disturbance class are 26 primary forest sites, 20 secondary forest sites, and 10 heavily disturbed, open sites.

Meta-analyses of separate correlations for the three Sphingid subfamilies (figure 6.8) do not show any significant differences between the taxonomic groups. Both Macroglossinae and Smerinthinae show overall significant positive effects, while the effect for Sphinginae fails to be significant according to the 95 percent confidence intervals, probably due to the reduced sample sizes in this small subfamily. All three subfamilies show no significant heterogeneity in data, with a weak trend (reminiscent of the Sphingidae as a whole) in the Macroglossinae ($Q_{T(df=55)}=66,7$, p=0,134) and no effect whatsoever in the two other subfamilies (Smerinthinae: $Q_{T(df=37)}=35,3$, p=0,550, Sphinginae: $Q_{T(df=18)}=7,0$, p=0,990). Thus, there appears to be no reason to suspect that differences in the range-abundance relationship between regions or disturbance classes (see above) are caused by different proportions of the subfamilies in the respective samples (see chapter 3.1 & 4.1).

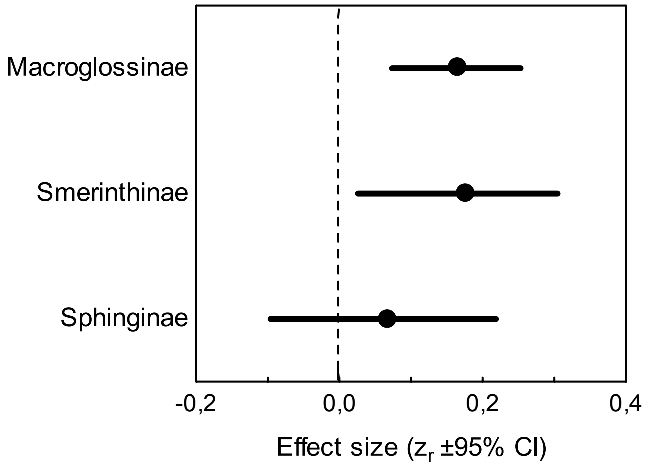


Figure 6.8 Average effect sizes and 95% confidence intervals (bootstrap) for Sphingidae subfamilies. Sites with less than 5 species were excluded, resulting in correlation data from 56 sites for Macroglossinae, 38 sites for Smerinthinae and 19 sites for Sphinginae. No independent contrasts were calculated for this analysis.

Partial range sizes yield ten positive range-abundance correlations (instead of eight for comprehensive data), the average effect size from meta-analysis (z_r [min., max. $95\%CI_{boot}$] =0,227 [0,150, 0,294]) is non-significantly larger than those for comprehensive ranges (see above).

Discussion

This study provides the first empirical support of a positive range-abundance relationship in tropical insects on a spatially extensive scale; i.e., comprehensive ranges of species (which cover most of the old world tropics in some species) and a subcontinent-wide extent of local abundance measurements were used. Most previous studies on tropical insects (e.g. dung beetles in Borneo: Hanski 1982, West-Africa: Hanski & Cambefort 1991; see also Krüger & McGavin 2000, Pantoja et al. 1995) covered considerably smaller regions and used partial ranges (i.e., the number of sampling sites where a species was found) as a measure of distribution. A number of studies on tropical butterflies, however, showed in a conservation-related context that the local rarity of species is usually associated with small geographical ranges (using comprehensive ranges from the literature, grouped in crude range classes). While the single studies were considering very small regions for abundance assessments (often comparing disturbed *vs.* undisturbed habitats), they indicate an overall trend for a positive range-abundance relationship across Southeast Asia (Vietnam: Spitzer et al. 1993, Thailand: Ghazoul 2002, Moluccas: Hill et al. 1995, Lesser Sunda Islands: Hamer et al. 1997; see also Thomas 1991 for Costa Rica).

For Sphingidae, positive range-abundance relationships were found for ordinal abundance assessments in several regions as well as for a summed effect of single-site correlations (in meta-analysis), but not for ‘conventional’ measures like mean or maximum abundance. The biological and methodological implications of these results will be discussed in detail below.

Missing species

For ordinal data analyses 284 species (239 night-active, 45 day-active taxa) were available, while mean abundance–range correlations included 132 species (in 16.373 specimens) and site-by-site correlations at 58 sampling stations covered 144 species (in 16.292 specimens). All species in quantitative data were contained in the ordinal data, thus highlighting the value of long-term surveys (see also DeVries et al. 1997). 380 species of hawkmoths are currently known from Southeast-Asia (of which 375 are formally described, Beck & Kitching 2004) – thus, ca. ¾ of all species found their way into analysis, while the rate drops to ca. 35 percent if only quantitative data were considered. On local sampling sites a week of high-intensity light trapping (as was applied in own sampling) yields ca. ¾ of the expected species at that site and time (see chapter 2). Only few studies used a complete monophyletic group for macroecological analysis (e.g. Gaston & Blackburn 1996), and the achieved ratio of analysed *vs.* regionally available species in this study is not bad if compared e.g. to 50 percent for British macrolepidoptera (Quinn et al. 1997b) that have been collected in considerably larger sampling programmes.

However, missing species are unlikely to be random selections from the assemblages with regard to targeted variables like distribution or abundance (Blackburn & Gaston 1998, Alpizar-Jara et al. 2004). Leaving aside collecting artefacts (e.g. species that are not drawn to light), which were discussed in chapter 2, it must be assumed that missing species represent the locally rare taxa or those with restricted ranges in regions that were not sampled. Aggregation seems to be stronger in rare than in common species (e.g. Gaston et al. 1998, Hubbell 2001 and references therein), which makes it likely that a rare species is not even found in a locally intensive survey unless it is carried out on a site where its population is concentrated. From Southeast-Asia a number of geographically very restricted species (e.g. endemics on small islands) are known (e.g. Beck & Kitching 2004, chapter 4.1). They are entirely missing from range-abundance analyses as no quantitative samples from the respective regions were available, partly because of their geographical isolation, but more often because of political constraints on visiting the respective regions.

If range-abundance relationships are assumed to be more or less triangular, as was frequently reported (e.g. Gaston et al. 2000, Thompson et al. 1998, Warren & Gaston 1997) and supported by null model simulations in this study, missing endemic species (which should be locally rare according to the hypothesis) could over-proportionally weaken the chance of finding a positive relationship in regression analysis. In line with this argument, 'funnel plots' (figure 6.9, Rosenberg et al. 2000) of sample size *vs.* effect size z_r indicate a dependency of raw data effect sizes on sample sizes (but not for contrast effect sizes). This N-z_r correlation is not merely a power-effect, which would influence p-values but not z_r. Thus, it should be expected that missing species bias results towards weaker positive relationships than would have been found in complete samples. Nonparametric tests were used to explore the potential of various parameters to produce such biases by assessing the influence of island identity, disturbance class and sample site elevation on the number of sampled species and specimens. No significant effects were found, although there are trends for influences on both variables by island identity (KW-Anova (N=58), specimens: $H_{df=7}$=11,9, p=0,104; species: $H_{df=7}$=13,5, p=0,060) and elevation (Spearman rank correlations (N=54), specimens: R=-0,258,

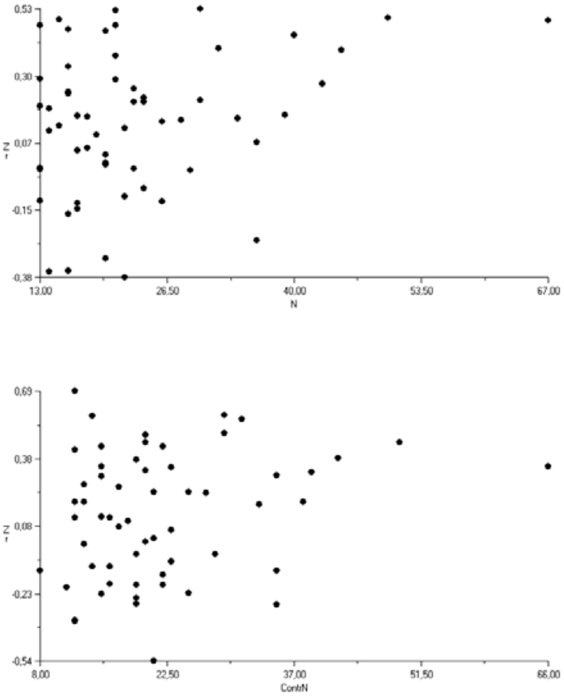


Figure 6.9 plots sample size N (number of species at local site) vs. the effect size z_r ('funnel plot'). With increasing N the sampling error of z_r decreases as expected (Rosenberg et al. 2000). However, z_r is not independent of N but is positively correlated for raw data (upper graph; log-transformed N, 58 sites: Pearson r^2=0,069, p=0,047), while this trend is lost in effect sizes of independent contrasts (lower graph; Pearson r^2=0,044, p=0,110).

p=0,060; species: R=-0,219, p=0,111), but not for disturbance class, latitude or longitude (p>0,15). Variable species numbers are partly a true effect of habitat and biogeography (see chapters 3.1 & 4.1), but can also be caused by different specimens numbers in samples (see e.g. figure 6.1). Such differences might occur due to varying site productivity, but are more likely to be an artefact of sampling conditions (weather, temperature, light type, etc., see above for references). Thus, there is a chance that effect sizes on some islands (particularly the Eastern ones) and at higher elevations are underestimated due to lower specimen numbers in samples. However, analyses based on independent contrasts do not show a dependency of species number on effect size, yet produce qualitatively the same patterns as raw data, so the mentioned biases cannot be solely responsible for the reported effects.

Rare species can also produce a bias in the other direction (i.e., they can produce artefact positive range-abundance relationship) if their rarity leads to a negative bias in range size assessments due to the lower likelihood of being discovered (e.g. Gaston et al. 2000, Gaston et al. 1997). Such effects can certainly not be excluded for Sphingidae data (see also Beck & Kitching 2004) and will be further discussed below.

Effects of measurement

a) Scale of range area

Ordinal data from several regions as well as meta-analysis of 58 sampling sites, indicate that comprehensive range areas yield slightly weaker range-abundance correlations than partial, Southeast-Asia-wide ranges. Boundary analysis from a null model simulation point into a similar direction, while this effect is not evident for correlations of range area and mean local frequency. Differences in analyses based on partial and comprehensive range measurements are not dramatically different in their overall results, which provides justification of utilising partial range measures as a proxy for lacking comprehensive range data (yet still on a subcontinent-wide scale, e.g. Europe-wide ranges in Quinn et al. 1997a, b). The extent of partial range measure in this study is probably well beyond a scale at which more localised processes than for comprehensive ranges, such as metapopulation dynamics (Hanski 1997), would have to be expected. However, there still appear to be consistent trends for stronger positive correlations if partial ranges were used. Thus, this effect has to be considered in the overall assessment of range-abundance relationships (see also Gaston 1996a).

b) Abundance measurement

Analyses of the range-abundance relationship based on local abundance samples (e.g. in meta-analysis of single sites) or regional commonness assessments (ordinal data for five regions) were generally either significantly positive or non-significant. Opposed to this, a non-significant negative pattern was found for mean frequency data, which became almost significant if independent contrasts were used (figure 6.4, table 6.4). Null model simulations, on the other hand, supported expected data boundaries of a positive, polygonal relationship, and a rank correlation, which was additionally calculated to acknowledge for the non-normality of log-transformed range data (see above) also indicated a non-significant positive trend. It might be futile to interpret the direction of a non-significant correlation, yet there appears to be a fundamental, methodologically important difference in local abundance measurements and their normalised means over a large spatial extent.

It has been suggested (K.J. Gaston pers. com.) that the use of frequencies (relative abundances instead of raw abundance) introduces an error as not frequencies but population sizes, or densities, are addressed by range-abundance theory. Using frequencies as a substitute makes the assumption that total Sphingid productivity does not vary across sites – which is certainly a gross oversimplification, although insular Southeast-Asia has, on a large scale, no huge gradients of light or water availability that would lead to great differences in primary production (see e.g. maps in Cramer et al. 1999). Raw abundances from light trapping, on the other hand, are certainly not comparable across sites due to strong, manifold proven effects of weather, moonlight and temperature conditions (e.g. Muirhead-Thompson 1991, Holloway et al. 2001, Yela & Holyoak 1997, McGeachie 1989). Raw abundances of moths from light trapping might be useful only in truly huge samples where varying conditions are levelled out across many sampling nights (as maybe in Quinn et al. 1997b).

However, it is unlikely that the observed discrepancy between local and mean abundance are caused by the potential flaws of frequency measures. Rather, it is probably due to habitat heterogeneity, which leads to different local abundances of species in various habitats and regions (see e.g. chapter 3.1) and hereby to a complex, multi-peaked spatial abundance distribution for which means, as well as maxima or single local figures, are no sensible measure (Brewer & Gaston 2003, Gaston 1996a, Hengeveld 1990). Similarly, Thompson et al. (1998) found no positive range-abundance relationship among British herbs on a regional or national scale, but when they analysed abundance within defined habitat types, significant correlations emerged. Holt et al. (2004) showed in a microcosm that habitat heterogeneity increased the residual variation in abundance-occupancy correlations *via* a decrease of biotic interactions. Meta-analysis appears as a suitable way to handle this problem, as it allows regressing range area with local abundance in each habitat, yet still yields a summarising, spatially extensive test result.

c) Phylogenetic correction

Acknowledging for effects of phylogenetic non-independence is by now a standard procedure for macroecological analyses (e.g. Blackburn & Gaston 1998, Brown 1999) although there is a lot of disagreement as to whether this is really necessary, and how it is done best. The application of independent contrast has been criticised for various reasons: It might not always be necessary or successful, to remove phylogenetic autocorrelation in data (Freckleton et al. 2002, Price 1997, Rheindt et al. 2004, Diniz-Filho & Torres 2002), the evolutionary model assumptions of the independent contrast method might be inferior to other methods under certain circumstances or with incompletely known phylogenies (Martins & Hansen 1997, Martins 1996, Losos 1994, Gittleman & Kot 1990, Harvey & Pagel 1991) and other factors than phylogeny, such as environmental history, might as well lead to non-independence of comparative data (Brown 1999). The ‘phylogeny’-substitute which was used here does not contain branch length information, it has many unresolved nodes and must generally be considered as approximate at most. Phylogenetic controls mostly lead to a reduction of significance, but conventional and independent contrast analyses seem generally highly correlated in their results (Garland et al. 1999). Here, major analyses were presented both for raw data and independent contrasts (as advised by Garland et al. 1999, Blackburn & Gaston 1998). A comparison of results shows that general findings are not greatly affected, whether raw data or contrasts were used – mostly, contrast data had weaker p-values and less positive correlation effects (as has been reported in many comparative studies, Garland et al. 1999). The only exception are the analyses of mean abundance data, where contrasts sometimes yielded stronger effects than raw data, both for correlations and null model simulations. Thus, without questioning the general necessity of acknowledging for and correcting (if possible) phylogenetic non-independence in comparative data, the application of independent contrast in this data set was not necessary, except for the virtue of knowing this fact. Several reasons might be responsible for this indifference, but cannot be sorted out at present: Weaknesses in data (as e.g. the rather inaccurate phylogeny) or the use of independent contrasts (which might not be the proper technique for tackling range area or frequency evolution) might have hindered a precise correction, or there is actually no important phylogenetic autocorrelation in the data (tests of phylogenetic independence on the transformed data were non-significant despite a trend for positive autocorrelation, see above).

Effects of region and habitat type

Meta-analysis was used to test for differences in the effect sizes of rang-abundance correlations along some *a priori* chosen parameters (region, habitat disturbance, elevation). No statistically different effect sizes between categories were found, yet the generally ‘directed’ trends could be indicative for a lack of power due to a too low number of sample sites, rather than no influence of the parameters: Significantly positive summarized effects could only be found in the Western part of the archipelago, or in primary habitats, but not East of ‘Weber’s line’ or in secondary or heavily disturbed sites. Samples from higher altitudes had overall weaker range-abundance relationships. Ordinal data analyses (e.g. table 6.1) support the finding of a geographical gradient if independent contrast data are considered (reassuringly in a methodological context, the non-significant relationship in Peninsular Malaysia is mirrored by a non-significant relationship for quantitative data at the site GEN1 (see appendix I), which is almost identical to where the ordinal data were collected). Various features of Sphingidae communities (e.g. regional species richness, proportion of subfamilies) are known to change along a Northwest-Southeast gradient throughout the Malesian archipelago (see chapter 4.1). For many tropical Southeast-Asian species, New Guinea and the Bismarck archipelago are an eastern distribution limit, as only few wet-tropical habitats can be found South and East of there – there is mainly desert (Australia) and water (South Pacific). It is yet unexplored how such a distribution limit can influence the shape of the range-abundance relation, compared to range extension possibilities in all directions. Biogeographical dispersal barriers such as deep sea straits lead to a lower similarity of the Eastern regions with the Asian mainland (see chapter 4.1), which is presumably the main source of species immigration for Sphingidae. It has yet to be explored if a lower immigration rate in the Eastern regions, as compared to the Western part of the archipelago, could lead to a higher average time that a species was present at the time of sampling (i.e., if Eastern Sphingid assemblages are older than Western ones; T. Hovestadt pers. com.). This might be expected under certain assumptions such as increasing local adaptation (see Kawecki & Ebert 2004 for a review), hence lower extinction probabilities, with persistence time in a region. If so, the higher extinction probabilities of rare and endemic species could have caused the weaker range-abundance relationships (Johnson 1998b) east of 'Weber's line'.

On a local scale, habitat disturbance as well as elevation was shown to influence community composition and subfamily proportions, but not overall diversity of hawkmoths (see chapter 3.1). Although no effects of subfamily association on the relations were found (see below), it might be interesting that positive range-abundance relations are found only in those categories of 'region' and 'habitat disturbance' that feature a relatively high proportion of Smerinthinae.

All three observed patterns – an West-East distinction, a habitat disturbance gradient and an influence of elevation of the sampling sites – appear to hold in a graphic display of multiple site classifications according to the three parameters (not shown), although low numbers of sampling sites per category lead to large confidence intervals for all classes. This indicates that the suggested effects are not merely an artefact of co-varying parameters. A proper test of these three suggested parameters is theoretically possible in meta-analysis (in a Generalized Linear Model, Rosenberg et al. 2000), but is not incorporated into the software that was used here. Furthermore, an overlap of confidence bands makes it likely that a larger number of sampling sites would be necessary to achieve statistical significance in such a model.

Differences between subfamilies

Clearly evident differences in habitat preferences (i.e., habitat disturbance, altitude, chapter 3.1), biogeography (dispersal, range position, chapter 4.1) and larval feeding niche (diversity of utilised host plants, chapter 5.1), but not range area (chapter 4.2) were found between the Smerinthinae on the one hand, and Macroglossinae and Sphinginae on the other hand, a division that is possibly linked to life-history differences and dispersal abilities between the taxa (see also chapter 1.2 & 7). These led to the vague expectation that differences between the taxonomic groups might be reflected by the range-abundance relationship as well (Gaston & Blackburn 2003). However, none of the various comparisons shows a clearly differing pattern between the groups (see e.g. figure 6.8).

Nevertheless, site-by-site analyses conducted separately for subfamilies revealed some significantly negative range-abundance relationships (Smerinthinae: two undisturbed highland sites in Borneo (PS, MUL1), Macroglossinae: a secondary growth site in Flores (BAJ3)), which were never found for pooled data. A meta-analytical comparison of the patterns with regard to disturbance, region and elevation between the two larger subfamilies (Smerinthinae & Macroglossinae) yields some interesting results. Both taxonomic groups repeat the pattern for pooled data with regard to habitat disturbance (see figure 6.7), but the weakening of range-abundance correlations with increasing elevation is stronger in the Smerinthinae ($N=33$, slope $t=-0{,}0004$, $p_{rand}=0{,}002$) than in Macroglossinae ($N=51$, slope $t=-0{,}0002$, $p_{rand}=0{,}025$). Furthermore, while Macroglossinae exhibit the same effect sizes over the regions where it could be measured (Borneo, Flores, New Guinea), a significantly negative effect for

Smerinthinae was found in Peninsular Malaysia (as judged by 95 percent bootstrap-confidence intervals), a 'normal' effect size is reported for Borneo, and an exceptionally (and significantly) larger positive effect was found on Flores, although both Peninsular Malaysia and Flores had just two sampling sites in analysis.

For the Smerinthinae, all New Guinea sampling sites were excluded from analysis due to very low species richness or no data at all: If there was an influence of range position (i.e., the decrease of Smerinthinae species richness as one moves Southeast through the archipelago, chapter 4.1) on the range-abundance relationship, it cannot be analysed for exactly the same reason (see also Blackburn & Gaston 1998). Some other studies also failed to find effects of life-history or dispersal ability on range-abundance patterns (e.g. Gaston & Blackburn 2003, Quinn et al. 1997b, Frost et al. 2004), while others found differences between taxa and life styles with regard to range-abundance patterns (e.g. Arita et al. 1990, Thompson et al. 1998).

Causal explanations of the range-abundance relationship

Gaston et al. (1997, 2000) have reviewed and evaluated a number of hypothetical mechanisms for a positive range abundance relationship. Two possible statistical artefacts were implied (Gaston et al. 1997, 2000): (1) Rare species might be missed in undersampled regions and therefore their range might be underestimated, and (2) data might be phylogenetically autocorrelated, which leads to spurious correlations. Both hypotheses can be ruled out as sole mechanisms for a positive range-abundance relationship as such was also found in doubtlessly complete data sets (see Gaston et al. 1997), experimental studies (e.g. Warren & Gaston 1997), and increasingly on data sets that were corrected for phylogenetic autocorrelation (see Gaston et al. 1997, 2000). In the present data set in Southeast-Asian hawkmoths, phylogenetic autocorrelation apparently plays only a minor role (see above), and phylogenetically corrected data confirm the existence of the relationship. However, undersampling of rare species must be assumed, as geographical range information is certainly not complete despite best efforts in a range estimation process which probably buffers much of the undersampling (chapters 1.3 & 4.1, Beck & Kitching 2004). As an indication for the potential of this artefact, attention might be drawn to the fact that own investigations in the Lesser Sunda Islands (a fairly undersampled region) revealed a number of species which would otherwise not have been estimated to be present there (appendix II). Similar sampling in other 'remote' regions (e.g. Moluccas, Laos, Vietnam, Burma/Myanmar) would probably yield similar range extensions. Thus, the sampling artefact could contribute to a positive range-abundance relationship, although it seems unlikely that it would be solely responsible for it.

The remaining proposed *biological* mechanisms receive empirical support from published studies at varying degrees (see box 6.2 for an overview; Gaston et al. 1997, 2000 provide a thorough evaluation and discussion), though many predictions of the respective mechanisms are not mutually exclusive or thoroughly testable on most available data sets. While there are certainly better, more complete data for general hypothesis testing (e.g. for temperate vertebrates, see above), it might be worthwhile to discuss what can be found out about the proposed mechanisms with regard to the Southeast-Asian Sphingidae.

The *range position hypothesis* can easily be refuted as it predicts no positive relationship for comprehensive ranges. Its general assumption that species' abundance declines towards the edge of its range could not be confirmed by maps of the distribution and local abundance for some of the most abundant species in this study (not shown: *Ambulyx canescens, Daphnusa ocellaris, Daphnis hypothous, Acherontia lachesis*), nor e.g. for British birds (Blackburn et al. 1999). However, range-abundance plots indicate a triangular shape as was predicted by this hypothesis, but a tendency for polygonal (as opposed to linear) relationships seems to be connected with a wide geographical extent of a study (Gaston et al. 1997) or with certain life histories (Thompson et al. 1998), which makes it likely that many mechanisms can lead to such a pattern.

The *niche-breadth hypothesis* refers to n-dimensional niche space which makes it practically untestable. Nevertheless, the dietary breadth of herbivorous insects is certainly an evolutionary important niche dimension (Denno et al. 1995, Mitter et al. 1991, Futuyma 1976, Colwell & Futuyma 1971) and has been previously used to test niche breadth effects on range-abundance relationships (Quinn et al. 1997b). Correlations of niche breadth with distribution or abundance were apparently only rarely found (Gaston et al. 1997, but see e.g. Thompson et al. 1999, Nieminen & Hanski 1998). Only two of the three predictions of this hypothesis (see box 6.2) can be properly addressed by data: Larval host plant breadth is clearly correlated with range area (see figure 6.10 for data, chapter 5.1 for data sources and further information on host plants), while a correlation with mean abundance is much weaker and non-significant if independent contrasts are considered (dietary breadth is phylogenetically autocorrelated, see chapter 5.1). Mean abundances are possibly no suitable

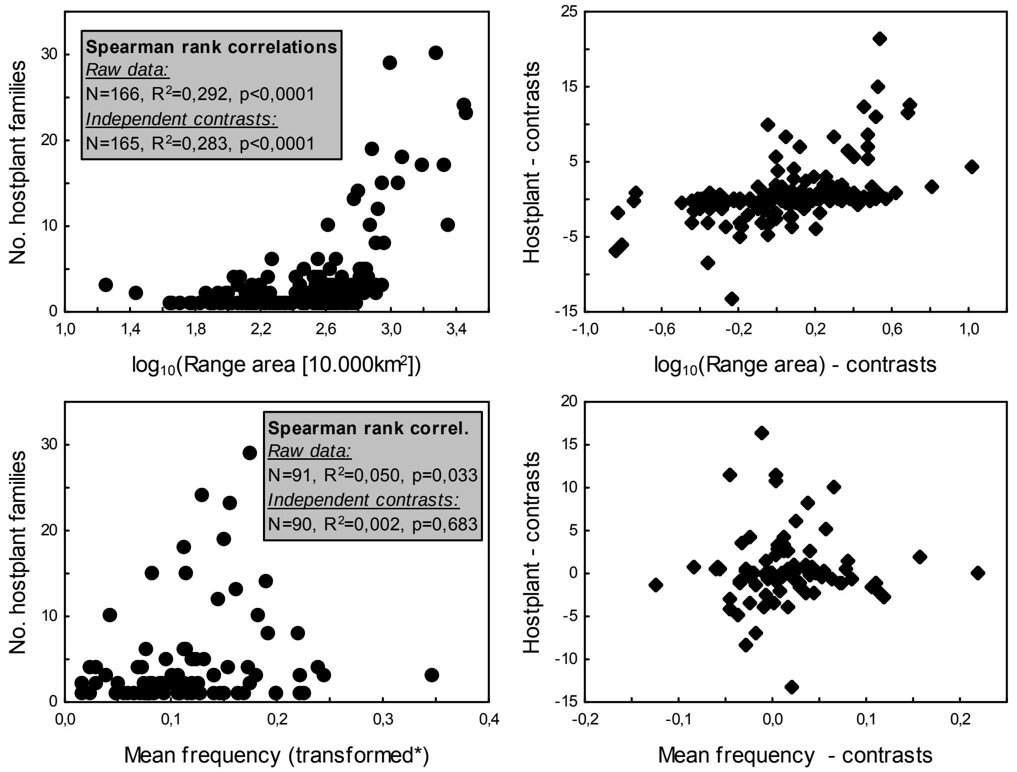


Figure 6.10 shows correlations of range area (upper) and mean frequency (*arcsin-sqroot*-transformed, lower) with the number of utilised larval host plant families for raw data (left) and independent contrasts (right; food plant data from I.J. Kitching (pers. com, see also Robinson et al. 2001a, b).

Box 6.2: Proposed biological mechanisms for a positive interspecific range-abundance relationship (PRAR) (from reviews in Gaston et al. 1997, 2000)

1) Range position

Mechanism: Species on the edge of their range in the study area are rarer, and have a smaller partial range than species which are in the centre of their range in the study area. Predictions: 1) Comprehensive range measures show no relation to abundance. 2) Rare and restricted species in a study are closer to the edge of their range than common and wide spread ones. 3) PRAR's are triangular, restricted species always have low abundance, while widespread species might have high or low abundance. Evidence: 1) Falsified by many comprehensive PRAR's, but apparently partial PRAR's are often stronger. 2) Some studies show this proposed effect. 3) Triangular patterns are commonly found, particularly in taxonomically inhomogeneous data and when range is measured as extent of occurrence. However, triangular patterns can be expected for other reasons as well.

2) Niche breadth

Mechanism: Species able to use a wide variety of resources can be geographically more widespread than those specialised on a (geographically) restricted resource. Furthermore, species with wide niches might be locally more abundant (this assumption is not undisputed, and it would exclude local adaptation). If so, a PRAR follows. Predictions: 1) Niche breadth correlates with geographical range and local abundance. 2) Possibly, if abundance is measured in atypical habitats a negative range-abundance relationship should result. 3) Widespread and abundant species are more likely to establish if they are introduced in a new environment. Evidence: 1) Most studies do not find a positive relation between niche breadth and local abundance/density, but n-dimensional niches make a complete test impossible. 2)+3) There is indication that the predictions might be true, but they are not exclusive to the 'niche breadth' hypothesis.

3) Resource availability

Mechanism: Local rarity and geographic restriction is a consequence of utilising locally rare and geographically restricted resources. Predictions: 1) Common & widespread species use common & widespread resources, rare species use rare resources. 2) Species which share a common resource do not exhibit a PRAR. 3) Resource specialists can be abundant and widespread. Evidence: 1) Some studies indicate that the abundance rank of phytophagous insect species is related to the abundance rank of their hostplants, which shifts the problem to another trophic level. There is also indication for the predicted pattern for other groups and resources. 2) Not tested. 3) Failure to document a positive relationship between niche breadth and abundance supports this prediction.

4) Density-dependent habitat selection

Mechanism: If species reach high population densities, they disperse and occupy more habitats (or patches) than when they live in low densities. If so, a PRAR follows. Predictions: 1) After major reductions in population size, species should have reduced ranges *and* occupy fewer habitat types. 2) This reduction in habitat type will follow the rank of habitat suitability, i.e. poorest habitats for the species will be given up first. 3) As populations decrease, populations in core habitats should have density-dependent increase in performance. Evidence: The hypothesis has been largely ignored, probably because it is difficult to test. Some taxa show density-dependent habitat selection, while many others probably do not.

5) Metapopulation dynamics

Mechanism: Denser populations (due to a higher species-specific carrying capacity) have a lower probability of extinction; therefore more patches in an environment are occupied with populations. Alternatively, a high number of occupied patches increases the probability of immigration in a given population, and hence lowers its extinction risk (rescue effect). Predictions: Several precise predictions of metapopulation dynamics can be found in Gaston et al.1997 and references therein. Evidence: The explanation should only apply to situations (taxa, habitats) where metapopulation dynamics are present – a difficult assessment as for most species data of population structure are not detailed enough for evaluation. Probably metapopulation dynamics are no explanation for the majority of taxa that exhibit PRAR's.

6) Vitality

Mechanism: Species differ in their response to spatially- and density-independent mortality factors (i.e., some species are more 'vital' than others). More resistant species will have higher local abundance, and occupy more sites. Predictions: After invasion of a species, its initial population growth will be a good predictor of its ultimate range size. Various other predictions involving birth rates can be found in Gaston et al. 1997, Holt et al. 1997. Evidence: Some studies indicate that species with smaller ranges have lower maximal population growth rates, but overall there is so far little evidence for predictions of this quite novel hypothesis.

measures of local abundance (see above), and host plant records are most probably incomplete and biased to an unknown degree and in an unknown direction (see discussion in chapter 5.1). Furthermore, the niche breadth hypothesis does not allow local food adaptation in polyphagous taxa (Gaston et al. 1997). Local specialisation has been suggested for many widespread, polyphagous insect taxa (e.g. Janzen 1988, see also Novotny et al. 2004), although no evidence for it could be found in data for the Southeast-Asian Sphingidae (chapter 5.1). Hawkmoth data tentatively support the prediction of niche-breadth correlating with range, and a correlation with abundance cannot be ruled out completely. Furthermore, the niche breadth hypothesis suggests that the measurement of species' abundance in 'uncommon' habitats leads to negative range-abundance relationships as such habitats favour specialists (Gaston & Lawton 1990). It was tried to test this idea for hawkmoths on Borneo by specifically sampling habitats that were defined *a priori* as 'rare' (based on vegetation composition and structure: Mangrove forests, heath forests (*keranga*), forest on ultrabasic soil). However, of five sites (two mangrove, two ultrabasic soil, and one highland heath forest) four yielded so few hawkmoths specimens that they could not be analysed at all, and the one remaining site (SIL1: primary forest on ultrabasic soil, see appendix I) did not show an unusual Sphingidae community compared to 'ordinary' primary forest sites. The range-abundance relationship for this site is indeed (non-significantly) negative (Pearson's r=-0,105, p=0,642), but little generality can be drawn from a single site. As a second test in this context it was assumed that disturbed sites were relatively rare habitats in the less populated parts of Southeast Asia until the onset of 'industrialized' logging ca. 50-70 years ago (e.g. Marsh et al. 1996, Monk et al. 1997). This might explain the reduced strength of range-abundance correlations in disturbed habitats, if one assumes that hawkmoth communities have not yet 'adapted' to the recent situation of large logged-over areas (e.g. Sodhi et al. 2004, Matthews 2002, Stibig et al. 2002, Jepson et al. 2001). It is difficult to assess how realistic this scenario is – for very slow dispersers such as termites, Pleistocene habitat differences (savannah *vs.* rainforest) are still evident in modern primary forest communities (Gathorne-Hardy et al. 2002b), while among the hawkmoths even very recent range extensions are known which are likely to be linked to anthropogenic habitat conversions (e.g. *Daphnis nerii* in Southeast-Asian suburban garden areas, Chey 2002b, I.J. Kitching pers. com.). As a third 'test', high elevations could be viewed as a 'rarer' habitat than lowland sites, although mountain ranges up to 2500 metres are not uncommon in most parts of Southeast-Asia, even on relatively small islands. This would explain the declining strength of the range-abundance relationship with increasing altitude. The third prediction of the niche breadth hypothesis, that widespread and abundant species are more likely to establish if newly introduced to a habitat, can be supported only anecdotically: Two species have successfully established on Hawaii during the last 30 years and were most likely introduced by human traffic: *Daphnis nerii* & *Macroglossum pyrrhosticta*. If sorted by declining rank, they are on place 7, respectively 17 of 380 for range areas, while ordinal abundance assessments (in Southeast-Asia) mostly place them in the upper mid-field in those regions where they occur.

The *resource availability hypothesis* is hard to test on existing data even if only larval host plant choice is considered as an important resource. No example was found where host plant family distribution limits a hawkmoth species' distribution (chapter 5.1, see also Quinn et al.

1997a, 1998), and there is indication that host plant specialists cannot be abundant and widespread (figure 6.10). Thus, the hypothesis is likely to be refuted.

Density dependent habitat choice hypothesis as well as the *metapopulation dynamics hypothesis* cannot be evaluated with the existing data, as local population processes are not sufficiently known. Furthermore, it is not clear what the proper spatial scales for such processes are for Sphingidae. Metapopulation dynamics are difficult to prove, but may commonly apply to herbivorous insects at various spatial scales (see review in Tscharntke & Brandl 2004, also Hanski 2004, Elmhagen & Angerbjörn 2001). Sphingidae are very mobile dispersers, so processes analogous to the rescue effect (e.g. Hanski 1997) could well occur on a large scale, e.g. between islands of the Malesian archipelago. Metapopulations dynamics in moths were found on islands at distances of up to ca. 20 kilometres in the Baltic Sea (Nieminen & Hanski 1998). Confirmed or very likely migrations occur in Southeast-Asian hawkmoth species only among the very widespread taxa (see chapter 4.2, figure 4.13), but it is not clear if migrations to temperate regions usually constitute 'population sinks' (which would mean that they must be backed by high population growth in the source populations, supporting both hypotheses), or if there are adaptive migrations systems as indicated e.g. for *A. convolvuli* in Africa and Europe (Gatter & Gatter 1990, Alkemeier & Gatter 1990). Confirmed migrating regions were not included in species' range measurements for the analyses presented here.

Similarly, very little can be said about the *vital rates hypothesis* due to the lack of data on species' population growth. However, the weak anecdotal support of recent immigrant on Hawaii (described under *niche breadth*) might also be applied to this hypothesis.

Additionally to these mechanisms reviewed by Gaston et al. (1997, 2000), two 'unified theories' predict and explain a positive range-abundance relationship from general model assumptions of demographic processes in neutral communities (Hubbell 2001) and by spatial abundance patterns (McGill & Collins 2003). While Hubbell's (2001) theory is not testable with the existing Sphingidae data in its detailed demographic assumptions (but see chapter 3.2 for further discussion), McGill & Collins' (2003) idea, which is in some respect related to the *range position hypothesis* (see above), is relatively straightforward: Based on the three premises that (1) species distributions are independent of each other, (2) global abundances of species follow a

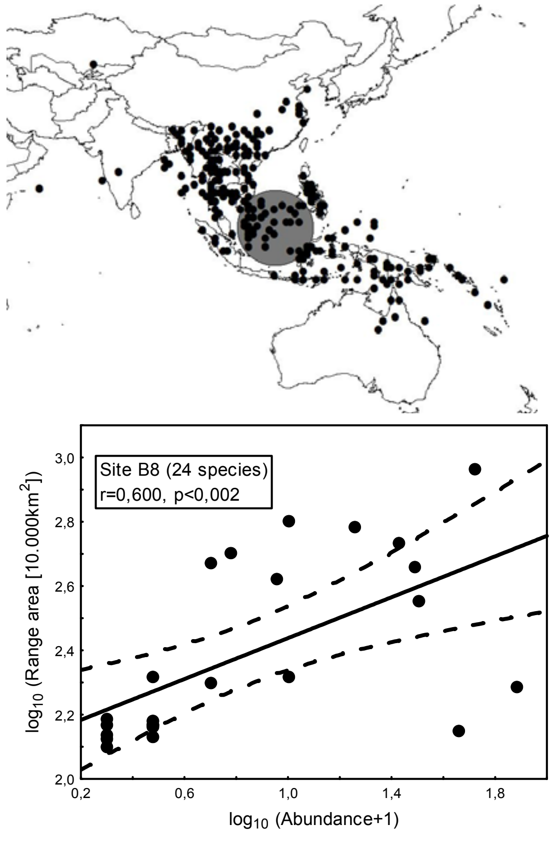


Figure 6.11: Species with distribution centres (see map: black dots) within a 1000km radius from North-central Borneo were tested for positive range-abundance relationships (see text for methods & results). One such relationship (B8) is exemplarily shown for comparison to the full data set in figure 6.5.

'hollow curve', and (3) abundance across a range follows a 'peak-and-tail' pattern (e.g., a Gaussian curve), they are able to model a positive range-abundance distribution, species-area relations, species turnover across space, and species-abundance distributions in a spatially large context (McGill & Collins 2003). Their idea relies on the overlap of species' ranges with different centres. If their model would be a sufficient explanation for range-abundance relationships, it should lead to the prediction that species with identical distribution centres should not exhibit a positive relationship. While this cannot be tested precisely with the present data, it can be attempted with several approximations: Distribution centres of all Southeast-Asian Sphingidae species were calculated as the mean of their latitudinal and longitudinal extremes (the centroids of each range would be more precise, but are difficult to compute for the fragmented areas of an archipelago). 'Identical centre' was broadly defined as those species with their distribution centre within a 1000 kilometres radius around Northern-central Borneo (as most local sampling sites were located in the northern half of Borneo). Only these species were used for range-abundance correlations at 42 local sites on Borneo (including a total of 34 species, see figure 6.11). The summarised effect size from meta-analysis is z_r [min., max. $95\%CI_{boot}$] = 0,278 [0,132, 0,401]. Thus, contrary to the prediction, it is not smaller but (non-significantly) larger than for all species (figure 6.6).

Several studies indicate that body size is a variable that interacts with range size (Biedermann 2003, Olifiers et al. 2004, Murray et al. 1998, Diniz-Filho & Torres 2002) and species' abundance (e.g. Hodkinson & Casson 2000, Maurer 1999, Basset & Kitching 1991), and might therefore influence the shape of the range-abundance relationship (e.g. Arita et al. 1990, see also Blackburn & Gaston 2001). However, data from the family Sphingidae, which have a relatively restricted range of body sizes if compared to taxonomically broader associations (see chapter 5.2), do not indicate an effect on mean local frequencies or range areas (figure 6.12, see also Johnson 1998a for a similar result on Australian mammals).

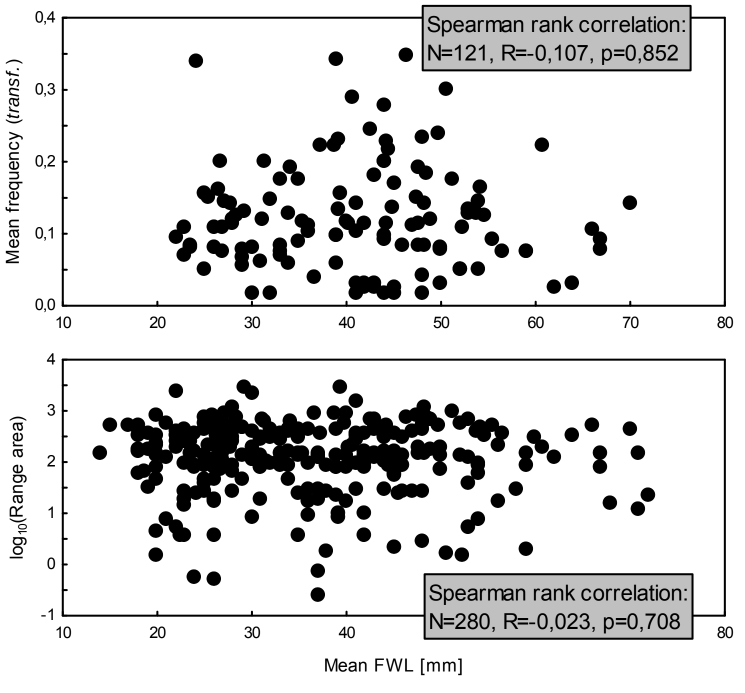


Figure 6.12: No relations of body size (as forewing lengths, FWL) with mean frequency (upper graph) and range size (lower graph) were found. Furthermore, null model simulations (10.000 runs) did not reveal significant data boundaries.

Johnson (1998b) has pointed out that over evolutionarily very long time-scales the range-abundance relationship within a taxon should become negative, as both low abundance and small range increase a species' extinction risk – species which carry both 'unfavourable' traits are unlikely to survive. The present hawkmoth data do not allow any comments on this, but possibly the enormous habitat destruction and associated extinctions in Southeast-Asia and elsewhere might be used to test the generality of the proposed process in ‘natural experiments’ in other taxa: If habitat destruction (and thus extinction rate) in a region is high, the left-over community (minus the newly immigrated disturbed habitat specialists) should exhibit a negative range-abundance relationship.

Conclusion

With various types of data a generally positive range-abundance relationship could be found for the Sphingidae of Southeast-Asia. Abundance measurement is a crucial point in analysis, and meta-analysis of single-site correlations is suggested as a suitable method to circumvent the problem of habitat heterogeneity. Apparently, there is an influence of geographical position, habitat disturbance and elevation on the strength of the relationship, while taxonomic affiliation, which is potentially linked to life-history, as well as body sizes have no impact. Of the proposed mechanisms for a positive range-abundance relationship, the *niche breadth hypothesis* (see Gaston et al. 1997) tentatively receives the strongest support from the data: Range sizes, and possibly also local abundance, are positively related to the number of utilised larval host plant families.

CHAPTER 7

SYNTHESIS AND GENERAL DISCUSSION

This study presented a macroecological analysis of the hawkmoths of Southeast-Asia as an example group for tropical herbivorous insects. Various analyses on methodology, local and regional community composition, niche parameters and the interspecific range-abundance relationship were carried out on the same system, applying similar methods and using largely the same data. Particularly the analysis of complex macroecological patterns such as the range-abundance relationship is certainly benefited by this approach, as it provides background information that would not be available otherwise, unlike e.g. in studies on temperate vertebrates. The finding of a weakening of the range-abundance relationship in Eastern sampling regions might serve as an example (see also below for further discussion): Biogeographical analyses generate new, explanatory hypotheses such as effects of declining species richness, greater isolation, etc. (see chapter 6).

The potential of the data and methods which were used here is certainly not yet exhausted. This applies especially to the estimates of geographic ranges of species, which provide rarely available, comprehensive and transparent distribution information. In future efforts, computerised GIS habitat models (see chapter 1.3 & 4.1 for references) could be calibrated on the Sphingidae ranges as presented here or on well known European ranges (e.g. by using random subsets of distribution records). Such work might result in a generally applicable Lepidoptera distribution model that may allows fast and relatively precise range estimates for other tropical Lepidoptera families. For many taxa a wealth of specimen-based distribution records are available, in some cases even in digital form (see also Graham et al. 2004). A number of analyses could then easily be repeated and furthered on other Lepidoptera families in the Southeast-Asian region, which would provide necessary replicates for the patterns that were suggested here (see below). Potential target groups in the near future might be day-flying butterflies or geometrid moths, for which large amounts of quantitative data are already available (see chapter 3.1 for references) or are currently in process (e.g. exhaustive samples of geometrid moths in Northern Borneo, J. Beck & Chey V.K. in prep.).

This work revealed a number of influential factors on the community structure of Southeast-Asian hawkmoths, which shall be reviewed and discussed here. Furthermore, it will be evaluated how further research work on this system could answer some newly arisen questions and investigate more of what so far has only been sketched about the macroecology of Southeast-Asian Lepidoptera.

Phylogeny

Phylogenetic relationships between hawkmoth taxa have been suggested to influence almost all investigated parameters of community organisation: With randomisation tests (Abouheif

1999) it was shown that the size of species' geographic range, their local abundance (albeit weaker) and their larval dietary niche breadth are phylogenetically autocorrelated. Furthermore, body sizes and reaction to habitat gradients and geographical position vary systematically between higher taxonomic units (such as subfamilies). Effects of phylogeny are far from unexpected: It is long acknowledged in comparative studies that many physiological and morphological traits are not phylogenetically independent (e.g. Harvey & Pagel 1991) and it is only logic to expect that such traits would also have an effect on the 'ecological level' of organisation, such as geographic ranges, population growth and -density or habitat preference. This is well exemplified by studies on Bornean forests, where phylogenetic effects on the community composition of trees were found (Webb 2000, Webb et al. 2002). Although this effect appears relatively trivial, especially in the light of historical biogeography, phylogenetic relationships have often been neglected in biodiversity research. Higher-taxon approaches or comparative studies are mostly presented in the context of biodiversity indicators (i.e., in order to minimise the sampling or determination effort in monitoring studies, e.g. Moritz et al. 2001, Williams & Gaston 1994, Williams et al. 1994, Lawton et al. 1998, Schulze et al. in press), instead of analytically asking which higher taxa do better or worse in a given habitat, and what the responsible common traits for these reactions are (see e.g. the discussion of life-histories in Begon et al. 1996).

A comprehensive phylogeny for Southeast-Asian Sphingidae is so far lacking and all analyses in this study were based on the taxonomic system as presented in Kitching & Cadiou (2000). While it seems unlikely that this tentative and in parts certainly incomplete surrogate produced major artefacts, it is possible that some interesting aspects of phylogenetic effects on community structure and biogeography (see below) were overlooked. Thus, a furthering of taxonomic and phylogenetic knowledge would certainly benefit the macroecologcial analyses of this taxon. The study has shown clearly that the immense importance of taxonomical expertise applies to far more than just presenting a name for a morphospecies (see also Wheeler 2004): Data compilations of various regions from multiple sources would be virtually impossible without confidence in the naming of specimens. Further ecological research could benefit taxonomical research by coordinating research sites and regions in order to collect material for morphological and genetic analyses from questionable populations or by supplying natural history information (e.g., do two morphs occur at the same time in the same habitat?) for species of unsure status.

Life history

Life histories are essential parameters for ecological traits such as population growth (Tammaru & Haukioja 1996), dispersal ability (e.g. Holloway 1998b) or 'weediness' (Sutherland 2004) of species. Their analysis in a comparative study is closely, sometimes inseparably associated with the analysis of phylogenetic differences in ecological traits (see above), as life histories are certainly often inherited and phylogenetically autocorrelated (Begon et al. 1996). In this study, a dichotomy between the hawkmoth subfamilies Smerinthinae on the one hand and Macroglossinae on the other hand has often been observed, while the considerably smaller subfamily Sphinginae appears tentatively rather associated with the Macroglossinae-patterns: Smerinthinae are generally less common and appear better adapted to stable, primary habitats (chapter 3.1), they might be less efficient dispersers, which has potential impacts in large-scaled patterns of species richness and biogeography (chapter 4.1), they utilise a more restricted spectrum of larval host plants (chapter 5.1) and have a consistently lower *thorax/wing length* ratio (chapter 5.2). Surprisingly, no effects of this dichotomy on the range-abundance relationship were observed (chapter 6). It has been suggested that these differences might relate to a life history distinction between *income breeders* (e.g. Macroglossinae, Sphinginae) and *capital breeders* (many Smerinthinae), which would serve well to explain some of the observed patterns. The alleged life history differences are mainly based on adult morphology, where missing proboscises in the tribus Smerinthini lead to the conclusion of a *capital breeding* life history. However, as explained elsewhere (e.g. chapter 1.2), the Smerinthinae-tribus Ambulycini shows in many respects similar ecological patterns as Smerinthini, while their proboscises are ‘reduced’ but fully functional. Thus, one necessity of further investigation on this topic will be to clarify the adult biology and life history of the Ambulycini and other, possibly paraphyletic (Kitching & Cadiou 2000) sub-groups of the Smerinthinae and to generally find empirical support for the conclusions drawn from proboscis reduction in the Sphingidae, i.e. lack of adult feeding, shorter adult life, larger female abdomens due to heavy egg loads, etc. Furthermore, widening the taxonomic breadth of the study to other Lepidoptera families might enable a replication of patterns for *income* and *capital breeding* taxa (see e.g. Tammaru & Haukioja 1996).

Disturbance

Anthropogenic habitat disturbance influences Southeast-Asian hawkmoth assemblages, although overall diversity is apparently unaffected (chapter 3.1). Furthermore, disturbance was also shown to affect the range-abundance relationship, which exhibits greater (positive) strength in primary habitats (chapter 6). The investigation of habitat disturbance must be a focal issue of tropical community ecology due to the pressing need for applicable knowledge to counteract landscape destruction by sustainable ecosystem management (see also chapter 1.1). Effects of disturbance on various Lepidoptera taxa have been investigated in great taxonomic and geographic breadth in the Indo-Australian tropics (see chapter 3.1 for references) and for some regions there exist even data on all major groups of Macrolepidoptera from the same sample sites (e.g. Holloway 1987b for Sulawesi, Holloway 1993b for Seram, Holloway 1976, 1984, Schulze 2000 for Borneo). A possibly fruitful line of further research would be to re-evaluate these pooled data in order to explore phylogenetic (see above) and life-history related causalities for the reaction of different groups to disturbance, e.g. by means of meta-analytical approaches.

Geographic gradients

The complex geography of the Indo-Australian region as well as its heterogeneous geological history is a two-sided feature for macroecological analyses in this region. On the one hand, it complicates all observed patterns due to nested communities, faunal discontinuities and the covariance of geographical parameters. This will make it difficult to compare empirical data to expectations or explanations from model approaches, be it explicit simulations or more or less precise ‘model’ ideas (e.g. Holloway 2003). On the other hand, this complexity gives the opportunity to observe differences or gradients in patterns which can provide valuable information on mechanisms. One frequently observed gradient in this study was not unexpectedly that from the West to the East of the Malesian archipelago. This gradient does not only influence species richness, subfamily proportions (see above) and patterns of faunal similarity (chapter 4.1), but also the strength of the range-abundance relationship which is only significantly positive in the Western part of the archipelago (chapter 6). This West-East gradient has at least two dimensions: a) a continuous effect of distance to the Asian mainland, which is most probably the source of immigration to the archipelago for Sphingidae, and b) a discontinuous effect by historically caused boundaries of faunal regions, such as Wallace’s, Weber’s or Lydekker’s line (chapter 4.1, see also e.g. Monk et al 1997). Analyses of phylogenetic biogeography would clarify geographic gradients in the region much better than similarity-based analyses (chapter 4.1), as they could account for different dispersal and speciation events of the various taxonomic subgroups in different times. Such an analysis, however, would require a phylogeny construction (see above) of the group as a first step. Widening the taxonomic breadth of analyses might help to understand the macroecological patterns along the West-East gradient (such as the weakening of the range-abundance relation), e.g. by comparing Asian taxa with those of Melanesian or Australian origin.

Zusammenfassung

In der hier präsentierten Arbeit wurden Häufigkeit und Verbreitung der Schwärmerarten Südostasiens (Lepidoptera: Sphingidae) sowie daraus resultierende Muster der Biodiversität, Biogeographie und Makroökologie untersucht. Verbreitungsnachweise der Arten wurden publizierten wie auch unveröffentlichten Artenlisten sowie Museumssammlungen (in enger Zusammenarbeit mit dem Naturkundemuseum London) entnommen. Über 34 500 Nachweise der weltweiten Verbreitung der 380 südostasiatischen Schwärmerarten (inkl. derer aus Neuguinea und von den Salomoninseln) wurden für GIS-gestützte Schätzungen der Verbreitungsgebiete verwendet, die unter *https://www.sphingidae-sea.biozentrum.uni-wuerzburg.de* zugänglich sind. Diese Internetseite präsentiert außerdem Bilder der Arten sowie Artenlisten für 114 Inseln des Malesischen Archipels. Die Häufigkeit der Arten wurde anhand nächtlicher Zählungen an künstlichen Lichtquellen abgeschätzt, wobei sowohl eigene Aufsammlungen als auch veröffentlichte und unveröffentlichte Daten anderer Sammler verwendet wurden. Für eine Analyse standen lokale Häufigkeitsdaten für 93 Standorte zur Verfügung, die insgesamt 17 676 Individuen aus 159 Arten umfassten.

Eine allgemeine Einleitung zur ‚makroökologischen' Forschung, der Suche nach Mustern der Gemeinschaftsökologie in großen räumlichen, zeitlichen und taxonomischen Bezugsrahmen, wird in *Kapitel 1* gegeben. Weiterhin wird ein Überblick über die Aspekte der Biologie der Lepidopterenfamilie Sphingidae gegeben, soweit diese in Zusammenhang zu Themen dieser Arbeit stehen, und die Eignung dieser Gruppe als Fallbeispiel für die makroökologische Analyse tropischer Insekten wird erörtert. Die Bedeutung interdisziplinärer Zusammenarbeit sowie die Notwendigkeit des Datenaustausches werden in diesem Zusammenhang hervorgehoben.

Methodisch relevante Aspekte des Lichtfanges wurden mit Hilfe von Wiederfangexperimenten markierter Falter sowie der Analyse quantitativer Aufsammlungen untersucht (*Kapitel 2*). Es gab keine Hinweise, dass Lichtquellen Falter aus weit entfernten Habitaten anziehen. Untersuchungen an 18 Arten der Familie Sphingidae, deren Häufigkeit für eine Analyse ausreichend war, ergaben keine Anhaltspunkte, dass diese unterschiedlich stark vom Licht angezogen werden. Dies ist von Bedeutung, da eine unterschiedliche Attraktion durch das Licht zu systematischen Fehlern führen würde, wenn man Lichtfangdaten als Maß für die relative Häufigkeit der Arten verwendet. Unterschiede in der Attraktivität des Lichts existieren jedoch zwischen taxonomisch und morphologisch sehr verschiedenartigen Taxa (z.B. verschiedenen Familien). Lichtfang ist eine geeignete und effektive Methode, die Artenzusammensetzung und relative Häufigkeit innerhalb von Schwärmertaxozönosen in Südostasien zu messen. Allerdings müssen Erfassungen die ganze Nacht über ausgeführt werden, um hohe Fangzahlen zu erreichen und systematische Fehler durch unterschiedliche Flugzeiten verschiedener Arten im Laufe der Nacht zu vermeiden.

Die lokale Artenvielfalt wurde an 57 Sammelstellen in Borneo verglichen (*Kapitel 3.1*). Es wurden keine Effekte anthropogener Habitatstörung auf die α-Diversität (gemessen als Fisher's α) beobachtet, jedoch unterschieden sich die Artenzusammensetzungen der Gemeinschaften signifikant in verschieden stark gestörten Habitaten. Höhe über NN, das Jahr der Aufsammlung und die Sammelmethode (ganze Nacht oder nur Teile der Nacht) wurden als weitere einflussreiche Parameter auf die Zusammensetzung der lokalen Gemeinschaften

identifiziert. Der Anteil der Unterfamilien in den Erfassungen unterscheidet sich in verschieden stark gestörten Habitaten: Smerinthinae nehmen entlang eines Gradienten vom Primärwald zu stark gestörten Flächen ab, während Macroglossinae den entgegengesetzten Trend zeigen. Zusammenhänge zwischen der Reaktion der Unterfamilien auf Störung und Höhe und Unterschiede in ihrem Lebenszyklus werden diskutiert.

Die Rang-Abundanz-Verteilungen in Aufsammlungen aus Südostasien (*Kapitel 3.2*) werden am besten mit der Lognormal-Verteilung beschrieben, obwohl die logarithmische Serie sich von den meisten Datensätzen ebenfalls nicht signifikant unterscheidet. Rang-Abundanz-Verhältnisse von regionalen (Mittelwerte für Arten) und lokalen Gemeinschaften (Mittelwerte für Ränge) folgen weitgehend jenen Mustern, die von Hubbell's (2001) neutralem Modell vorhergesagt werden, obwohl die mittleren Häufigkeiten der Arten durch ihre Phylogenie autokorreliert sind – d.h. die Arten sind nicht ökologisch neutral, sondern haben ererbte Eigenschaften, die zu einem gewissen Grad ihre lokale Häufigkeit bestimmen. Die Daten könnten eine Reihe von methodisch bedingten Fehlern enthalten, etwa durch die Verwendung zusammengefasster Daten aus heterogenen Gemeinschaften oder der Annahme ähnlicher Habitatproduktivität (in bezug auf Schwärmer) über die Sammelstellen hinweg.

Die großen Muster von Artenvielfalt und Biogeographie wurden für die Schwärmer des Malesischen Archipels untersucht (*Kapitel 4.1*). Die geschätzte Artenvielfalt der Inseln in der Region wird von Inselgröße und biogeographischer Assoziation beeinflusst. Arten-Areal-Beziehungen in doppelt-logarithmischer Darstellung sind nicht linear für die gesamte, heterogene Region, nur für manche der homogeneren Teilregionen ist Linearität erkennbar. Der Anteil der Arten verschiedener Schwärmerunterfamilien verändert sich mit der geographischen Lage der Inseln. Der Zusammenhang von Faunenwechsel zwischen Inseln und der Entfernung dieser Inseln voneinander ist steiler für Smerinthinae als für andere Unterfamilien. Diese Unterschiede werden im Lichte der unterschiedlichen Lebenszyklen der Unterfamilien diskutiert. Analysen der Faunenähnlichkeiten der Inseln zeigen im Grossen und Ganzen „lehrbuchmäßige“ Muster der biogeographischen Assoziation, wobei die „Wallace-Line“ die wichtigste Diskontinuität in der Fauna der Region darstellt. Weitere Analysen zeigen, dass die historische Geographie eine wichtige Determinante der Faunenähnlichkeit ist, moderne Dispersionsereignisse jedoch ebenfalls einen Grossteil der heutigen Schwärmerverbreitung erklären können.

Maße für die geographische Verbreitung verschiedener Auflösung und räumlichen Ausmaßes wurden verglichen (*Kapitel 4.2*). Verbreitungsmaße zeigen eine schiefe Verteilung mit vielen geographisch beschränkten und wenigen weitverbreiteten Arten. Eine kleine Anzahl von Arten hat ungewöhnlich große Verbreitungsgebiete. Eine Rangfolge der Arten nach GIS-gestützten Verbreitungsflächen-Schätzungen unterscheidet sich nicht stark von der nach gröberen Maßen (kleinste konvexe Polygone, Längen- und Breitengrad-Ausdehnung, Produkt aus Längen- und Breitengrad-Ausdehnung). Gesamt-Verbreitungsgebiete und Teil-Verbreitungsgebiete innerhalb Südostasiens sind miteinander korreliert, bereits in diesen recht großen Teil-Verbreitungsgebieten verändert sich die Reihenfolge der Arten jedoch deutlich. Andere Maße der Teil-Verbreitung abnehmender geographischer Ausdehnung zeigen eine zunehmende Schwächung der Korrelationen mit der Fläche des Gesamtverbreitungsgebietes, bleiben jedoch statistisch hochsignifikant. Verbreitungsgebietsgrößen von Arten sind phylogenetisch autokorreliert: Verwandte Gruppen von Arten haben ähnlich große Verbreitungsgebiete.

Larvale Wirtspflanzenbeziehungen standen für 44 Prozent der beschriebenen Schwärmerarten der Region zur Verfügung und wurden auf dem Niveau von Pflanzenfamilien analysiert (*Kapitel 5.1*). Schwärmer erscheinen als eine relativ polyphage Gruppe, zumindest wenn Nachweise aus verschiedenen geographischen Regionen zusammengefasst werden: Von 28 Prozent der Arten kennt man Fraßnachweise an vier oder mehr Pflanzenfamilien. Wirtspflanzen aus 112 Familien sind bekannt, die am häufigsten nachgewiesenen Pflanzenfamilien sind Rubiaceae, Vitacea und Aracea. Die Breite der „Nahrungsnische" trägt ein deutliches phylogenetisches Signal, d.h. eng verwandte Arten nutzen eine ähnliche Anzahl an Wirtspflanzenfamilien. Die durchschnittliche Breite der Nahrungsnische unterscheidet sich zwischen taxonomischen Gruppen der Schwärmer: Einige Arten der Unterfamilie Sphinginae nutzen eine deutlich höhere Anzahl an Pflanzenfamilien als andere Schwärmergruppen. Eine multidimensionale Skalierung der Wirtspflanzenfamilien zeigt, dass Smerinthinae-Arten wie auch der Sphinginae-Tribus Sphingini eine eng umgrenzte Gruppe von Wirtspflanzen nutzt, die in das Wirtspflanzenspektrum der Macroglossinae eingebettet scheint (d.h. mit jenem überlappt, im Gegensatz zu Darstellungen in der früheren Literatur), während Mitglieder des Sphinginae-Tribus Acherontiini aus dem „üblichen" Wirtspflanzenspektrum der Schwärmer hervorstechen und sowohl ungewöhnlich viele als auch andere Pflanzenfamilien im Vergleich zu anderen Sphingidenarten nutzen. Dies wird durch die Erkenntnis bestätigt, dass die Diversität genutzter Pflanzen (gemessen als Fisher's α der Wirtspflanzenfamilien) der Smerinthinae signifikant niedriger ist als die der anderen Unterfamilien. Es wurde kein Beispiel gefunden, wo die Verbreitungsgrenze einer Wirtspflanzenfamilie mit der einer Schwärmerart zusammenfällt und daher für die Ausbreitung des Falters limitierend sein könnte. Mögliche systematische Fehler in den Daten durch unvollständige Wirtspflanzennachweise werden diskutiert und müssen ernst genommen werden, die Ergebnisse sollten daher als vorläufig betrachtet werden.

Die Körpergrößen für 281 Schwärmer wurden als mittlere Vorderflügellänge gemessen (*Kapitel 5.2*). Ihre Verteilung ist leicht links-schief (d.h., es gibt mehr kleine als große Arten) und kann durch eine Lognormal-Verteilung beschrieben werden. Die Verteilung ist jedoch bimodal, was vermutlich durch systematische Größenunterschiede zwischen den Unterfamilien Macroglossinae und Smerinthinae hervorgerufen wird. Verteilungen lokaler Taxozönosen zeigen keine einheitliche Schiefe und können durch eine Normalverteilung beschrieben werden. Unterschiede von Habitat und Region können die beobachteten Unterschiede in der mittleren Körpergröße lokaler Taxozönosen nicht erklären. Die Verteilung der Körpergrößen zeigt keine Regelmäßigkeiten, die auf die Wirkung von Konkurrenz in der Gemeinschaft hinweisen würden.

Eine positive Beziehung zwischen lokaler Abundanz und geographischer Verbreitung konnte für die Sphingidae Südostasiens aufgezeigt werden (*Kapitel 6*). Dies ist der erste Nachweis einer derartigen Beziehung für tropische Insekten unter Verwendung des gesamten Verbreitungsgebietes der Arten und lokalen Häufigkeitsmessungen subkontinentalen Ausmaßes. Die Messung der „Häufigkeit" ist ein entscheidender Punkt der Analyse: Während unter Verwendung von Mittelwerten der lokalen Häufigkeiten der Arten keine Häufigkeits-

Verbreitungs-Beziehung zu finden ist, ist diese unter Verwendung lokaler Häufigkeitsdaten präsent. Metaanalyse von Korrelationen innerhalb der Daten einzelner Sammelstellen wird als eine geeignete Methode vorgestellt, mit der das Problem der Habitatheterogenität bei der Messung von Häufigkeit umgangen werden kann. Kontrolle für die gemeinsame Phylogenie der Arten (unabhängige Kontraste) wie auch die Verwendung der südostasiatischen Teil-Verbreitungsgebiete (anstatt der globalen Maße) verändern die Ergebnisse nicht wesentlich. Offenbar haben geographische Lage, Habitatstörung und Höhe über NN einen Einfluss auf die Stärke der Beziehung, während taxonomische Zugehörigkeit (die potentiell mit dem Lebenszyklus und der Verbreitungsfähigkeit zusammenhängt) wie auch Körpergrößen keine eindeutigen Wirkungen haben. Von den vorgeschlagenen kausalen Mechanismen der Häufigkeits-Verbreitungs-Beziehung wird die „Nischenbreiten-Hypothese" vorläufig am stärksten durch die hier analysierten Daten gestützt: Die Größen der Verbreitungsgebiete sind mit der Anzahl larvaler Wirtspflanzenfamilien positiv korreliert, während diese mit der gemittelten Häufigkeit nur schwach und anhand phylogenetisch korrigierter Daten überhaupt nicht in Beziehung steht.

Eine allgemeine Diskussion und Synthese der Ergebnisse sowie ein Ausblick über mögliche weiterführende Forschungen in diesem System sind in *Kapitel 7* zu finden. Die Anzahl erfasster Individuen und Arten sowie Details zu allen quantitativen Lichtfangstellen sind im Anhang zu finden, zudem wird eine Liste von lokalen Neunachweisen von Arten durch eigene Sammeltätigkeit in Malaysia und Indonesien präsentiert. Gedruckte Versionen dieser Arbeit enthalten auch eine CD-ROM mit *Version 0.99* der Internetseite „The Sphingidae of Southeast-Asia" (Internetadresse zur neuesten Version: siehe oben).

Summary

This study investigates the abundance and geographic distribution of the hawkmoth species (Lepidoptera: Sphingidae) of Southeast-Asia and analyses the resulting patterns of biodiversity, biogeography and macroecology. Data on the distribution of species were retrieved from published and unpublished faunal lists and museum collections (in close cooperation with the Natural History Museum, London). Over 34,500 records of the global distribution of the 380 species that occur in Southeast-Asia (including New Guinea and the Solomon Islands) were used for a GIS-supported estimate of distributional ranges, which can be accessed at *http://www.sphingidae-sea.biozentrum.uni-wuerzburg.de*, an Internet site that also provides pictures of the species and checklists for 114 islands of the Malesian region. The abundance of species in local assemblages was assessed from nightly collections at artificial light sources. Using a compilation of own samples as well as published and unpublished data from other sources, local abundance data on 93 sites are available for analysis, covering 159 species or 17,676 specimens.

A general introduction to the 'macroecological' research agenda, the empirical search for patterns in community ecology over large spatial, temporal and taxonomic scales, is given in *chapter 1*. Furthermore, an overview over features of the biology and natural history of the lepidopteran family Sphingidae, as far as they are relevant for topics of this study, is presented, and the suitability of this taxon as a 'case study' for the macroecological analysis of tropical insects is discussed. In this context, the importance of inter-disciplinary collaboration and data sharing is highlighted.

Methodologically relevant issues of light-trapping were analysed in Mark-Release-Recapture experiments as well as from quantitative descriptive samples (*chapter 2*). There are no indications that light trapping 'draws' specimens from far-away habitats to the sampling site. Furthermore, no proof was found that species within the family Sphingidae are differentially drawn to light (testing 18 species which were sufficiently common for analysis); differential attraction would lead to biases if light-trapping data is used as a measure of relative abundance in the habitat. Such biases, on the other hand, probably exist between taxonomically or morphologically more diverse taxa, e.g. different families. Light-trapping is an effective means of assessing species composition and relative abundances of Sphingid assemblages in Southeast-Asia, but sampling has to be carried out all night in order to maximise catch size and avoid biases due to different nightly flight times of the species.

Local biodiversity was compared in 57 habitats on Borneo (*chapter 3.1*). No effects of anthropogenic habitat disturbance on the within-habitat diversity (measured as Fisher's α) were observed, but the faunal composition of assemblages differs significantly under varying degrees of disturbance. Altitude, the year of sampling and the sampling regime (full night vs. part of the night) were identified as further parameters that influence the composition of local samples. The frequency of subfamilies in samples varies under different disturbance regimes: Smerinthinae decline along a gradient from primary habitats to heavily disturbed sites, whereas Macroglossinae show the reversed trend. Connections between the reactions of subfamilies to disturbance and altitude and life-history differences between the subfamilies are discussed.

The rank-abundance distributions (RAD) from samples across Southeast-Asia (*chapter 3.2*) are best fitted by the lognormal distribution, whereas the logseries distribution also does not deviate significantly from most data. Rank-abundance distributions of regional (means per species) and local assemblages (means per rank) largely follow the patterns which are predicted by Hubbell's (2001) neutral model, although mean frequencies of species are phylogenetically autocorrelated – i.e., species are not ecologically neutral, but carry traits that, to a certain extent, determine mean local abundance. Data may contain a number of methodologically caused biases, such as using pooled data of heterogeneous assemblages, and assuming equal habitat productivity (of hawkmoths) across sampling sites.

Major patterns of species richness and biogeography were investigated for the hawkmoths of the Malesian archipelago (*chapter 4.1*). Estimated species richness of islands in the region is influenced by island size and biogeographical association. Species-area relationships are (on a double logarithmic scale) not close to linearity for the whole, heterogeneous region, whereas they are so only for some of the more homogenous sub-regions. Species proportions of Sphingid subfamilies change with the geographic position of islands, faunal turnover of islands in relation to distance between the islands is steeper for Smerinthinae than for other subfamilies. These differences are discussed in the light of life history differences between the subfamilies. Phenetic analyses of island fauna similarities reveal, on a large scale, 'textbook'-like patterns of biogeographical associations with Wallace's line emerging as main faunal discontinuity in the region. Further analyses indicate that historical features of geography are an important determinant of faunal similarity, but that recent dispersal could also explain a significant portion of today's Sphingidae distribution.

Measurements of geographic range size of different resolution and geographical extent were compared (*chapter 4.2*). Range size measurements exhibit a strongly right-skewed frequency distribution with many geographically restricted species and fewer wide-spread taxa. A small number of species has idiosyncratically large ranges. Rankings from GIS-supported range size assessments do not deviate much from coarser measurements such as minimum convex polygons, latitudinal and longitudinal extents or their products. Comprehensive ranges and partial Southeast-Asia-wide ranges are correlated, but already at this rather large partial scale the ranking of species can change considerably in comparison to global ranges. Other measures of occupancy at increasingly smaller partial scales show decreasing strengths of correlations but remain highly significant. Range area data are phylogenetically autocorrelated: Related groups of species have ranges of similar size.

Larval host plant relationships for 44 percent of the described hawkmoth species in the region were available and were analysed on the level of plant families (*chapter 5.1*). Sphingidae appear as a relatively polyphagous group, at least if records of a large geographical region are pooled: 28 percent of the species are known to feed on four or more host plant families. Host plants from 112 plant families were recorded, the most commonly recorded plant families are Rubiaceae, Vitaceae and Aracea. Diet breadth of species carries a significant phylogenetic signal, i.e. closely related species utilise a similar number of host plant families. Average diet breadth differs between Sphingid taxa: Sphinginae, and here particularly the species of the tribus Acherontiini, utilise a significantly larger number of plant families than other Sphingid sub-groups. A multidimensional scaling plot of host plant relationships reveals that Smerinthinae species, as well as the Sphinginae-tribus Sphingini, use a tight group of host plants which are nested in the host plant spectrum of Macroglossinae (rather than non-overlapping, as has been suggested in earlier literature), whereas some members of the Sphinginae-tribus Acherontiini stand out from the 'usual' host plant spectrum of hawkmoths by using more host taxa and also different plant families than other Sphingidae. In confirmation of this, the diversity of utilised host plants among Sphingid families (measured as Fisher's α of host plant families) is significantly lower in Smerinthinae than in other subfamilies. No examples of host plant family range edge coinciding with hawkmoth range edge (hence possibly limiting it) were found. Potential biases of data due to incomplete host records are discussed and must be considered: results should be treated as tentative.

Body size data for 281 Southeast-Asian species were measured as mean forewing lengths (*chapter 5.2*): Their frequency distribution is slightly right-skewed (i.e., there are more small species) and can be described by a lognormal distribution. However, the distribution is bimodal, which is probably caused by systematic size differences between the subfamilies Macroglossinae and Smerinthinae. Local assemblages do not show a consistent skew and can be fitted by a normal distribution. No effects of habitat or region could be found that would explain observed differences in mean species size between local samples. The distribution of body size does not show any regularity which would indicate competition effects.

A generally positive range-abundance relationship could be documented for the Sphingidae of Southeast-Asia (*chapter 6*). This is the first report of this relationship for tropical insects using comprehensive range measures and a sub-continental extent of abundance measurements. Abundance measurement appears as a crucial point in the analysis: Means of local frequencies do not produce a range-abundance relationship, whereas local measures do. Meta-analysis of single-site correlations is suggested as a suitable method to circumvent the problem of habitat heterogeneity in abundance measurements. Phylogenetic controls (independent contrasts) as well as the use of partial range measures of Southeast-Asia-wide extent do not change results greatly. Apparently, there is an influence of geographic position, habitat disturbance and elevation on the strength of the relationship, whereas taxonomic affiliation (which is potentially linked to life-history and dispersal ability) as well as body sizes have no clear impact. The 'niche breadth hypothesis' tentatively receives the strongest support of the proposed mechanisms for a positive range-abundance relationship from the data: Range sizes are positively related to the number of utilized larval host plant families, while the correlation with mean local abundances is weak and does not persist on phylogenetically corrected data.

A general discussion and synthesis of results as well as an outlook on further research on this system is presented in *chapter 7*. Numbers of collected specimens and species as well as further details on all quantitative light trapping sites is given in the appendix, which also contains a list of range-extending species records from own sampling in Malaysia and Indonesia. Printed versions of this thesis also contain an added CD-ROM with *version 0.99* of the Internet site "The Sphingidae of Southeast-Asia" (see above for URL to the most recent version).

Ringkasan dalam Bahasa Malaysia

Kajian ini adalah mengenai spesis rama-rama 'hawkmoth' (Lepidoptera: Sphingidae) yang wujud di Asia Tenggara dari aspek limpahan dan keluasan geografi, serta corak biodiversiti, biogeografi dan makroekologi. Data taburan spesis ini diperolehi daripada senarai fauna yang diterbitkan atau belum diterbitkan serta daripada koleksi Muzium Natural History di London. Lebih 34,500 rekod taburan global bagi 380 spesis 'hawkmoth' ditemui di Asia Tenggara (termasuk Papua New Guinea dan kepulauan Solomon) telah digunakan untuk sistem maklumat geografi (GIS) di mana anggaran julat taburan spesis tersebut boleh diperolehi, dengan melayari internet di alamat *http://www.sphingidae-sea.biozentrum.uni-wuerzburg.de*, yang mana, di laman web tersebut ada menyediakan gambar-gambar spesis tersebut dan senarai spesis di 114 Gugusan Kepulauan Melayu. Pengumpulan limpahan spesis dijalankan pada waktu malam dengan menggunakan kaedah sumber cahaya lampu. Dengan menggunakan data-data himpunan peribadi dan sumber- sunber lain sama ada diterbitkan atau belum diterbitkan, limpahan data setempat di 93 kawasan kajian dianalisis, yang mana ianya meliputi 159 spesis 'hawkmoth' atau 17,676 spesimen.

Pengenalan am kepada agenda penyelidikan secara makroekologi diterangkan di dalam Bab 1 mengenai kajian empirikal ke atas corak keluasan ruang, masa dan skala taksonomi di dalam ekologi komuniti. Sebagai tambahan, turut diterangkan ialah gambaran keseluruhan ke atas ciri-ciri biologi dan pengetahuan semulajadi bagi famili Sphingidae serta topik- topik yang relevan dan juga perbincangan mengenai kesesuaian takson famili sebagai 'kajian kes' untuk menganalisis serangga-serangga tropika secara makroekologi turut dijalankan. Dalam konteks ini, penekanan diberikan ke atas kepentingan kerjasama disiplin dalaman dan perkongsian data.

Isu-isu berkaitan dengan kaedah sumber cahaya lampu juga dianalisis di dalam kaedah eksperimen 'Tanda-Tangkap-Tangkap Semula' serta daripada penghuraian jumlah sampel (kebanyakannya daripada Borneo Utara, Bab 2). Kaedah sumber cahaya lampu ini tidak memberi kesan terhadap spesimen dari habitat jauh 'mendekati' kawasan kajian. Tambahan pula, tiada bukti yang menunjukkan perbezaan spesis bagi famili Sphingidae mempunyai kesan kepada tarikan untuk menghampiri cahaya lampu (menguji 18 spesis yang umum untuk dianalisis), di mana ia mendorong untuk berlakunya ralat sekiranya data kaedah sumber cahaya lampu digunakan untuk mengukur limpahan relatif di dalam habitat tersebut. Selain itu, kesan-kesan ralat mungkin wujud di antara famili-famili dari segi taksonominya ataupun morfologinya. Di Asia Tenggara, kaedah sumber cahaya lampu merupakan cara berkesan untuk menafsir kandungan spesis dan limpahan relatif komuniti Sphingidae, dan proses pengumpulan sampel harus dijalankan pada setiap malam secara berturut-turutan untuk memperolehi jumlah saiz tangakapan maksimum dan mengelakkan wujudnya ralat berikutan dengan perbezaan dalam masa penerbangan antara spesis pada waktu malam.

Biodiversiti tempatan yang dijalankan di 57 kawasan habitat di Borneo telah dibandingkan (Bab 3.1). Gangguan habitat antropogen tidak memberi kesan ke atas diversiti-α (diukur sebagai α-Fisher), tetapi komuniti komposisi fauna menunjukkan perbezaan nyata di dalam pelbagai jenis peringkat gangguan. Altitud, koleksi tahunan dan regim pengumpulan sampel (malam penuh berbanding sebahagian malam) turut mempengaruhi komposisi sampel-sampel tempatan. Kekerapan sub famili di dalam sampel adalah berbeza bergantung kepada jenis-

jenis gangguan: Smerinthinae semakin berkurangan di kawasan gangguan habitat yang tinggi, di mana Macroglossinae menunjukkan kesan yang sebaliknya. Turut dibincangkan di sini ialah, hubungan di antara reaksi sub famili terhadap kawasan-kawasan gangguan habitat, altitud dan corak hidup di antara sub famili dibincangkan.

Taburan peringkat limpahan (rank-abundance distribtuions [RAD]) sampel daripada Asia Tenggara (Bab 3.2) adalah paling sesuai digunakan dalam taburan log normal di mana, ia juga sesuai digunakan dalam kebanyakan data taburan siri-siri log. Taburan peringkat limpahan bagi kawasan (min per spesis) dan komuniti tempatan (min per peringkat) menunjukkan corak-corak yang telah diramalkan oleh model neutral Hubbell (2001), meskipun kekerapan min spesis adalah menyerupai autokorelasi filogenetik-iaitu, spesis adalah tidak neutral secara ekologinya, tetapi membawa ciri-ciri yang pada tahap tertentu, menentukan min kekerapan tempatan. Data mungkin mengandungi beberapa ralat, semasa menggunakan data kumpulan bagi komuniti heterogenus dan semasa memberi andaian produktiviti (rama-rama 'hawkmoth') dalam habitat adalah sama sepanjang kawasan-kawasan koleksi sampel.

Corak-corak kekayaan spesis dan biogreografi yang utama bagi rama-rama 'hawkmoth' di Gugusan Kepulauan Melayu dikaji selidik (Bab 4.1). Dianggarkan kekayaan spesis di dalam kawasan tertentu dipengaruhi oleh saiz setiap pulau dan hubungan biogeografinya. Hubungan antara spesis dengan kawasan adalah tidak selari (pada skala logaritma) bagi seluruh kawasan heterogenus dan juga di sub-sub kawasan yang lebih homogenus. Peratus spesis bagi setiap sub famili Sphingidae berubah mengikut kedudukan geografi setiap pulau, perbezaan fauna berhubung dengan jarak di antara setiap pulau adalah lebih curam bagi subfamili Smerinthinae berbanding dengan sub-sub famili lain. Perbezaan ini dibincangkan dari segi perbezaan corak hidup setiap sub famili Sphingidae. Analisis-analisis persamaan fauna antara setiap pulau tidak menunjukkan perubahan baru dalam hubungan corak biogeografi, ini bermaksud garisan Wallace adalah sempadan utama yang membezakan fauna-fauna yang wujud di bahagian Barat dan Timur sempadan tersebut. Sejarah geografi Asia Tenggara merupakan faktor utama dalam menentukan persamaan fauna-fauna, namun demikian penyebaran baru-baru ini turut mempengaruhi taburan Sphingidae masa kini.

Pengukuran ke atas saiz keluasan geografi menggunakan resolusi yang berbeza dan pada skala geografi ada dibandingkan (Bab 4.2). Pengukuran saiz keluasan menunjukkan graf taburan frekuensi dengan spesis yang bergeografi terhad dan sebaran keseluruhan spesis dalam kuantiti kecil mencondong ke kanan. Kedudukan keluasan kawasan yang diukur menggunakan GIS tidak memberi perbezaan ketara daripada ukuran secara kasar seperti poligon-poligon berkecerunan cembung yang minimum (minimum convex polygons), takat longitud dan latitud atau hasil darab daripada takat longitud dan latitud. Jumlah keluasan dan sebahagian Asia Tenggara berkorelasi antara satu sama lain, namun demikian kedudukan spesis boleh berubah. Pengukuran dari skala-skala kecil memberi kesan korelasi yang lemah tetapi korelasi masih ketara. Saiz keluasan data adalah autokorelasi secara filogeni: Kumpulan spesis yang berhubungkait mempunyai keluasan yang hampir sama.

Hubungan antara larva dan tumbuhan perumah bagi 44 peratus rama-rama 'hawkmoth' di Asia Tenggara hanya di analisis pada peringkat famili tumbuhan sahaja. Sphingidae mengamalkan sistem pemakanan polifagi, di mana 28 peratus daripada spesis tersebut memakan empat atau lebih jenis famili tumbuhan. Sebanyak 112 famili tumbuhan telah direkodkan, di mana famili tumbuhan seperti Rubiaceae, Vitaceae dan Araceae merupakan pilihan utama larva Sphingidae. Purata pengambilan pelbagai jenis famili tumbuhan adalah berbeza di antara sub-sub famili Sphingidae. Sub famili Sphinginae, terutama sekali kumpulan Acherontiini, memakan lebih banyak famili tumbuhan berbanding sub-sub kumpulan Sphingid yang lain. Plot-skala berbentuk multidimensi (MDS) untuk hubungan tumbuhan perumah menunjukkan spesis Smerinthinae mempunyai tumbuhan perumah yang terhad berbanding dengan spesis Macroglossinae. Taburan tumbuhan perumah tidak mempengaruhi taburan rama-rama 'hawkmoth' di Asia Tenggara. Data tumbuhan perumah adalah kurang lengkap dan keputusan dianggap sebagai keputusan sementara.

Data saiz badan bagi 281 spesis di Asia Tenggara diukur sebagai min kepanjangan sayap hadapan (Bab 5.2): Taburan fekuensi sedikit condong ke kiri (menunjukkan bahawa spesis kecil lebih banyak) dan boleh digambarkan menggunakan taburan log normal. Walaubagaimanapun, taburan adalah berkecerunan dwimod disebabkan oleh saiz secara sistematik di antara sub-subfamili Macroglossinae dan Smerinthinae. Komuniti tempatan tidak memberi pesongan yang tetap dan boleh ditunjukkan menggunakan taburan normal. Habitat dan kawasan tidak memberi kesan untuk membandingkan min saiz badan spesis dengan sampel- sampel tempatan. Perbezaan dari segi saiz badan juga tidak menunjukkan kewujudan kesan persaingan.

Hubungan positif keluasan-limpahan bagi Sphingidae di Asia Tenggara telah dibuktikan (Bab 6). Ini merupakan hubungan pertama bagi serangga-serangga tropika menggunakan keseluruhan keluasan spesis dan mengukur kekerapan dalam skala benua kecil dilaporkan. Ukuran limpahan amat penting dalam analisis: Purata kekerapan tempatan tidak menghasilkan hubungan keluasan-limpahan, manakala ukuran tempatan menunjukkan perhubungan. Analisis-Meta digunakan sebagai kaedah menyelesaikan masalah dalam mengukur kekerapan di kawasan habitat heterogenus. Kawalan filogenetik (independent contrasts) atau ukuran keluasan sebahagian daripada Asia Tenggara tidak dapat mengubah keputusan. Hubungan ini dipengaruhi oleh kedudukan geografi, jenis-jenis gangguan habitat dan ketinggian tetapi tidak dipengaruhi oleh taksonomi (berkaitan dengan corak hidup dan keupayaan penyebaran) atau saiz badan. Saiz keluasan berkait rapat secara positif dengan famili tumbuhan perumah larva. Walaubagaimanapun, korelasi dengan purata taburan tempatan adalah lemah dan tiada korelasi langsung apabila menggunakan data yang diperbetulkan untuk filogeni.

Perbincangan terhadap keputusan yang diperolehi, serta kajian yang boleh dilanjutkan daripada topik ini dihuraikan di dalam Bab 7. Jumlah koleksi spesimen dan spesis, serta butir-butir selanjutnya berhubung kawasan-kawasan koleksi sampel dan senarai-senarai spesis yang ditemui di Malaysia dan Indonesia boleh dilihat di bahagian lampiran. Versi cetakan tesis ini boleh didapati dalam bentuk CD-ROM versi 0.99, melalui alamat internet "The Sphingidae of Southeast-Asia" (versi terkini boleh dilihat di atas).

Ringkasan dalam Bahasa Indonesia

Kajian ini membahas tentang jenis-jenis Lepidoptera dari keluarga Sphingidae (‘hawkmoth’) yang terdapat di Asia Tenggara, terutama tentang sebaran geografis dari masing-masing jenis (biogegrafi), serta pola keanekaragaman dan kelimpahan jenis di berbagai tempat (‘makroekologi’). Data sebaran jenis-jenis ini diperoleh dari berbagai sumber, baik yang telah ataupun yang belum diterbitkan serta koleksi Musium Natural History di London. Lebih dari 34,500 catatan sebaran global 380 jenis ‘hawkmoth’ yang ditemui di Asia Tenggara (termasuk Papua New Guinea dan kepulauan Solomon) telah disertakan dalam penaksiran sebaran masing-masing jenis dengan menggunakan sistem informasi geografis (GIS) di mana sekarang sebaran jenis-jenis tersebut dapat diketahui di *http://www.sphingidae-sea.biozentrum.uni-wuerzburg.de*. Alamat ini menyediakan gambar-gambar jenis tersebut serta daftar jenis dari 114 pulau dalam Kawasan Melayu. Penaksiran kelimpahan jenis dilakukan berdasarkan hasil penangkapan pada waktu malam hari dengan menggunakan cahaya lampu. Dari hasil penangkapan yang dilakukan oleh penulis sendiri maupun orang lain lain, baik yang telah diterbitkan ataupun yang belum, telah dilakukan analisis terhadap kelimpahan jenis setempat di 93 tempat dalam kawasan tersebut, yang mana meliputi 159 jenis ‘hawkmoth’ atau 17,676 spesimen.

Dalam Bab 1 disajikan pengenalan tentang bidang kajian ‘makroekologi’, yaitu sebuah upaya empiris untuk melihat pola-pola dalam ekologi komunitas yang meliputi sebuah ruang, waktu serta lingkup taksonomis yang sangat luas. Selain itu, akan diberikan gambaran umum atas ciri-ciri biologi dan sejarah hidup keluarga Sphingidae, sejauh hal-hal ini sesuai dengan topik-topik dalam kajian ini. Juga, kesesuaian keluarga ini untuk dipergunakan dalam kajian makroekologi, terutama dalam kaitannya dengan serangga tropis. Dalam konteks ini, akan dibahas pentingnya kerjasama interdisipliner dan tukar-menukar data untuk kepentigan kajian ini.

Hal-hal yang berkaitan dengan metodologi, terutama tentang penangkapan dengan cahaya, dianalisis berdasarkan hasil percobaan-percobaan Mark-Release-Recapture dan cuplikan-cuplikan diskriptif kuantitatif (Bab 2).). Tidak dijumpai tanda-tanda bahwa cahaya lampu “menarik” serangga yang dimaksudkan dari tempat-tempat yang berjauhan dari tempat dimana perangkap dipasang. Selain itu juga tidak ditemukan adanya perbedaan ketertarikan terhadap cahaya lampu diantara jenis-jenis Sphingidae (percobaan dengan 18 jenis yang memadai untuk sebuah analisis), satu hal yang patut dipertimbangkan mengingat hal ini dapat menyebabkan penyimpangan. Penyimpangan seperti ini kemungkinan dijumpai apabila pembahasan menyertakan kelompok taksonomi yang lebih beragam serta bentuk tubuh yang beranekaragam pula (misalnya, dari berbagai keluarga). Penangkapan dengan cahaya merupakan sebuah cara efektif untuk menaksir komposisi jenis dan kelimpahan relatif dari masing-masing jenis Sphingidae di Asia Tenggara. Meskipun demikian, memang sebaiknya penangkapan dilakukan dilakukan sepanjang malam untuk menghindari bias yang disebabkan oleh adanya perbedaan waktu terbang antara jenis.

Dalam Bab 3.1. dapat dijumpai perbandingan pola keanekaragaman jenis di 57 lokasi di Borneo. Dari kajian ini, tidak ditemukan adanya dampak perubahan habitat yang disebabkan oleh manusia (berdasarkan nilai α-Fisher), tetapi ditemukan perbedaan nyata komposisi jenis di dalam berbagai komunitas lokal apabila dikaitkan dengan peringkat gangguan atau perubahan habitatnya. Disamping itu ketinggian lokasi, tahun dilakukannya penangkapan serta cara penangkapan (semalam penuh, sepertiga atau setengah malam) turut mempengaruhi komposisi komunitas lokal. Hal ini terutama dapat dilihat dari adanya perbedaan kekerapan anak keluarga (subfamili) yang terkait dengan jenis-jenis gangguan: Smerinthinae cenderung semakin berkurang di kawasan-kawasan yang telah mengalami banyak gangguan, sedang Macroglossinae menunjukkan kesan sebaliknya. Untuk menerangkan perbedaan ini, dalam bab yang sama dibahas pengaruh sejarah hidup masing-masing anak keluarga tersebut dalam kaitannya dengan tanggapan mereka terhadap gangguan habitat serta ketinggian.

Dalam kajian ini ditemukan bahwa rank-abundance distributions (RAD) dari cuplikan-cuplikan dari berbagai tempat di Asia Tenggara (Bab 3.2) sangat sesuai dengan sebaran log normal, sedang sebaran log seri tidak menyimpang secara signifikan dari sebagian besar data. RAD pada tingkat kawasan (rerata per jenis) dan komunitas lokal (rerata per rank) umumnya mengikuti pola seperti model netral yang diusulkan oleh Hubbell (2001), meskipun rerata kekerapan jenis dengan sendirinya menunjukkan hubungan filogenetis. Artinya, jenis-jenis tidak memiliki kenetralan ekologis, melainkan membawa sifat-sifat yang hingga batas-batas tertentu menyebabkan kelimpahan lokal. Meskipun demikian perlu diingat bahwa data-data yang dipergunakan dalam kajian ini boleh jadi mengandung bias metodologis, seperti misalnya dipakainya ‘pooled data’ dari komunitas-komunitas heterogen dan penganggapan kesetaraan produktifitas serangga yang diteliti di semua tempat pengumpulan.

Dalam Bab 4.1. diungkapkan tentang pola-pola kekayaan jenis dan biogeografi Sphingidae di Kepulauan Malesia. Hasil-hasil penaksiran kekayaan jenis di berbagai pulau di kawasan ini dipengaruhi oleh luasan pulau dan asosiasi biogeografis yang ada. Hubungan antara jumlah jenis dan luas pulau ternyata tidak linear (pada skala dua logaritma) untuk semua tempat di dalam kawasan yang heterogen, tetapi mendekati linear pada tempat-tempat yang lebih homogen. Perbandingan jenis dari anak-anak keluarga (subfamily) Sphingidae berubah, tergantung dari posisi geografis pulaunya. Selain itu, ‘turnover’ jenis dalam kaitannya dengan jarak antar pulau tampak lebih curam pada Smerinthinae dibanding dua anak keluarga yang lain. Perbedaan ini dibahas dengan melihat perbedaan sejarah hidup dari masing-masing anak keluarga tersebut. Analisis fenetik terhadap persamaan-persamaan yang dapat ditemukan pada jenis-jenis yang dijumpai di sebuah pulau mengungkapkan adanya asosiasi biogeografis seperti yang banyak dikenal dalam berbagai buku ajar, dimana Garis Wallace menjadi pemutus kontinyunitas fauna di kawasan ini. Analisis lebih jauh menunjukkan bahwa sejarah geografis di kawasan ini menentukan persamaan-persamaan jenis Sphingidae antara pulau. Meskipun demikian, persebaran di masa yang lebih kini dapat pula menerangkan sejumlah besar sebaran jenis-jenis Sphingidae seperti yang kita jumpai saat ini.

Penaksiran kisaran geografis dalam berbagai resolusi dan skala geografis telah diperbandingkan (Bab 4.2.). Hasil-hasil penaksiran kisaran menunjukkan kecondongan kuat ke kanan dalam sebaran kekerapan, terutama terdiri dari jenis-jenis yang memiliki sebaran geografis sempit dan sedikit jenis yang memiliki sebaran luas. Jenis-jenis tertentu diketahui memiliki kisaran benar-benar luas dan khas. Hasil penentuan peringkat luas kisaran dengan menggunakan GIS ternyata tidak banyak menyimpang dari hasil-hasil yang diperoleh dari penaksiran menggunakan cara-cara yang lebih ‘kasar,’ seperti ‘minimum convex polygons’ dari perhitungan batas-batas garis lintang maupun bujur. Terdapat hubungan antara kisaran keseluruhan dengan kisaran parsial di Asia Tenggara. Meskipun demikian, pada kisaran parsial yang cukup besar ini peringkat jenisnya dapat berubah sesuai dengan kisaran global. Pengukuran lain dari penempatan kisaran yang semakin kecil menunjukkan bahwa kekuatan dari hubungan-hubungan ini masih sangat berarti. Data tentang luas kisaran ternyata dengan sendirinya terkait menurut filogenetisnya: Jenis-jenis yang berkerabat cenderung memiliki luas kisaran yang sama.

Hubungan larva dan tumbuhan inang dari sekitar 44 % jenis Sphingidae yang dikenal di Malesia sudah cukup banyak didokumentasikan dan dalam kajian ini catatan-catatan yang ada dianalisis pada tingkat keluarga tumbuhan (Bab 5.1). Sphingidae tampaknya merupakan kelompok serangga polifag, setidaknya apabila dianalisis berdasarkan catatan-catatan yang terkumpul dari kawasan geografis yang luas: 28% jenis yang ada diketahui memakan empat atau lebih tumbuhan inang. Dalam hal ini, tumbuhan inang dari 112 keluarga tumbuhan telah tercatat, yang paling umum adalah Rubiacae, Vitaceae dan Araceae. Kemajemukan pakan suatu jenis serangga membawa satu pertanda adanya hubungan filogenetis, yaitu jenis-jenis serangga yang berkerabat dekat cenderung memakan jenis-jenis tumbuhan dari keluarga-keluarga yang sama pula. Selain itu, terdapat perbedaan rerata tingkat kemajemukan pakan antar masing-masing anak keluarga Sphingidae: Sphinginae ,terutama sekali dari marga Acherontiini, memiliki jumlah tumbuhan inang yang jauh lebih banyak dibanding kelompok-kelompok lain. Dengan menggunakan ‘multidimensional scaling plot’ dari berbagai jenis tumbuhan inang dapat diketahui bahwa jenis-jenis Smerinthinae serta jenis-jenis Sphinginae dari marga Sphingini, memakan sejumlah tumbuhan inang tertentu yang ternyata juga merupakan sebagian jenis tumbuhan yang dimakan oleh Macroglossinae (sebelumnya disebutkan dalam literature bahwa kedua kelompok tumbuhan inang ini tidak tumpang tindih). Sementara itu, sejumlah anggota Sphinginae dari marga Acherontiini merupakan kelompok yang memakan jauh lebih banyak taksa tumbuhan sebagai inang dibandingkan kelompok-kelompok yang lain dalam keluarga Sphingidae. Sesuai dengan kenyataan ini, keanekaragaman tumbuhan inang yang dimakan anak-anak keluarga ini (diukur sebagai Fisher’s α tumbuhan inang) secara berarti lebih rendah pada Smerinthinae dibanding kedua anak keluarga lainnya. Sejauh ini tidak dijumpai adanya kesesuaian antara batas persebaran keluarga-keluarga tumbuhan inang ini dengan batas persebaran jenis-jenis Sphingidae. Selanjutnya dibicarakan tentang kemungkinan-kemungkinan terjadinya bias yang diakibatkan oleh tidak lengkapnya catatan tentang tumbuhan inang tersebut. Dianjurkan agar hasil analisis ini diterima sebagai hasil sementara.

Tubuh dari 281 jenis di Asia Tenggara diukur berdasarkan rerata panjang sayap depan (Bab 5.2): Sebaran kekerapan hasil pengukuran menunjukkan kecondongan ke kiri, artinya lebih banyak jenis yang berukuran kecil sehingga dapat ditampilkan sebagai sebaran log normal. Meskipun demikian, sebaran ini bimodal. Hal ini kemungkinan disebabkan oleh perbedaan ukuran sistematis di antara anak-anak keluarga (sub-subfamili) Macroglossinae dan Smerinthinae. Komunitas lokal tempatan tidak menunjukkan pola yang tetap dan membentuk sebaran normal. Tidak dijumpai adanya pengaruh habitat ataupun kawasan yang dapat menjelaskan perbedaan rerata ukuran tubuh antara cuplikan-cuplikan lokal. Sebaran ukuran tubuh ini tidak menunjukkan keteraturan sebagai tanda adanya pengaruh persaingan.

Secara umum terdapat hubungan positif antara kisaran dan kelimpahan jenis-jenis Sphingidae di Asia Tenggara (Bab 6). Hal ini baru pertama kali ini dilaporkan, terutama dalam kaitannya dengan serangga tropis dengan menggunakan ukuran-ukuran kisaran secara menyeluruh dan dalam skala anak benua (subkontinental). Cara penaksiran kelimpahan tampaknya merupakan penentu dalam analisis ini: Rerata dari kekerapan lokal tidak menghasilkan hubungan kisaran-kelimpahan, sedang perhitungan berdasar kekerapan menghasilkan hubungan ini. Oleh karena itu, disarankan agar digunakan meta-analisis berdasarkan hubungan yang ada pada suatu tempat (‘single-site correlation’) untuk menghindari masalah yang terkait dengan heterogenitas habitat dalam penaksiran kelimpahan. Kendali fologenetis (‘indipendent contrast’) serta penggunaan kisaran parsial dalam skala Asia Tenggara tidak menyebabkan perubahan hasil-hal perhitungan secara nyata. Tampaknya terdapat pengaruh posisi geografis, gangguan terhadap habitat dan ketinggian tempat terhadap kuat-lemahnya hubungan tersebut. Sedangkan afiliasi taksonomis (yang kemungkinan berkaitan dengan sejarah hidup dan kemampuan menyebar) serta ukuran tubuh tidak menunjukkan pengaruh yang nyata. Hipotesis ‘kemajemukan relung’ sementara ini memperoleh dukungan terkuat untuk menerangkan mekanisme terbentuknya hubungan positif kisaran-kelimpahan dari data: Ada hubungan positif antara luas kisaran dengan jumlah tumbuhan inang, sedang hubungannya antara kelimpahan lokal lemah atau bahkan tidak ada sama sekali apabila kita mengaitkannya dengan aspek filogenetis.

Sebuah pembahasan secara umum dan rangkuman dari hasil-hasil kajian ini serta sebuah pandangan tentang kelanjutan kajian ini diuraikan di dalam Bab 7. Jumlah spesimen yang dikumpulkan dan jenis yang ditemukan berikut perincian hasil kuantitatif penangkapan pada masing-masing tempat disajikan dalam lampiran. Perincian ini juga meliputi sebuah daftar catatan perluasan kisaran dari hasil tangkapan penulis sendiri di Malaysia dan Indonesia. Tesis ini dilengkapi sebuah CD-ROM versi 0.99 tentang “The Sphingidae of Southeast-Asia” yang juga bisa ditemukan di internet di alamat yang disebutkan di depan.

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Würzburg, 21. Januar 2005

(Jan Beck)

Ehrenwörtliche Erklärung

gemäß §4 Abs. 3 Ziff. 3, 5 und 8
der Promotionsordnung der Fakultät Biologie der
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Hiermit erkläre ich ehrenwörtlich, dass ich die vorliegende Dissertation selbstständig angefertigt habe und kein anderen als die angegebenen Quellen und Hilfsmittel verwendet habe.

Die Dissertation wurde bisher weder vollständig noch teilweise an einer anderen Hochschule mit dem Ziel, einen akademischen Grad zu erwerben, vorgelegt.

Am 30. September 1998 wurde mir von der Universität Würzburg der akademisch Grad „Diplom-Biologe Univ.“ verliehen. Weitere akademische Grade habe ich weder erworben noch versucht zu erwerben.

Würzburg, 21. Januar 2005

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Jan Beck

Appendix I: Details for all Southeast-Asian light-trapping sites with quantitative data for 20 or more specimens. Latitude & longitude is given in metric format, minimum precision for site locations is ±0,5°. Own sampling sites (J. Beck) are marked with an asterisk (*).

Region	Site	Lat.	Long.	Elevation	Primary	Secondary	Heavily dist.	N	S_{obs}
Borneo	B1	4,5	114,5	50			x	89	16
	B2	4,5	114,5	110		x		187	32
	B3	4,5	114,5	200	x			295	30
	B4	4,5	114,5	50			x	86	21
	B6	4,5	114,5	110	x			116	21
	B7	4,5	114,5	125	x			416	34
	B8	4,5	114,5	320	x			1478	50
	B9	4,5	114,5	325	x			296	26
	BAR	-0,1	114,0		x			175	36
	BRU-Ed	4,6	117,8	250			x	105	20
	BRU-Ga	4,6	117,8	250			x	20	9
	BRU-Pf	4,6	117,8	250			x	84	17
	BRU-SF	4,6	117,8	400		x		557	36
	BT	5,5	116,5	1200	x			58	23
	CRO1*	5,4	116,1	1171	x			968	39
	CS-POR1	6,1	116,7	580	x			325	29
	CS-POR3	6,1	116,7	600	x			47	6
	CS-POR7	6,1	116,7	460			x	77	11
	DER-I	5,3	117,3	100		x		22	10
	DV1*	5,0	117,8	220	x			899	30
	DV1a*	5,0	117,8	220	x			22	7
	DV2*	5,0	117,9	263		x		266	17
	DV3*	5,0	117,9	220		x		56	17
	DV4*	5,0	117,8	340		x		129	23
	INT1*	3,4	116,7	150		x		25	10
	INT2*	3,4	116,8	150	x			31	11
	K	5,5	116,5	2110		x		34	15
	KIN1*	5,4	118,0	120		x		22	7
	KIN2*	5,4	118,0	120		x		94	22
	KU	5,5	116,5	1050		x		33	13
	LPS1*	4,4	115,7	1497	x			69	16
	LPS3*	4,4	115,7	1059		x		107	20
	MUL1	4,5	114,4	1790	x			70	15
	MUL14	4,5	114,4	1000	x			22	13
	MUL17	4,5	114,4	50	x			122	21
	MUL23	4,5	114,4	250	x			23	10
	MUL25	4,5	114,4	900	x			21	11
	MUL8	4,5	114,4	150	x			36	14
	POR1*	6,0	116,7	580	x			166	26
	POR7*	6,0	116,8	366			x	23	12
	POR8*	6,0	116,8	350			x	1746	43
	POR-TWW	6,0	116,7	500	x			36	14
	PS	5,5	116,5	1930	x			62	19
	RS	5,5	116,5	2600	x			63	16
	S1	3,5	113,5	20		x		86	16
	S3	1,5	110	720	x			1159	45
	S4	3	113	410	x			23	5
	S5	1,5	109,5	240	x			82	16
	S6	1,5	109,5	60		x		155	24
	S7	4,5	115	100		x		558	40
	S8	4,5	115	320	x			41	6
	SAY2	6,2	116,5	808			x	46	22

Appendix I – continued

Region	Site	Lat.	Long.	Elevation	Primary	Secondary	Heavily dist.	N	S_{obs}
Borneo	SER2c*	6,3	116,7	270	x			23	6
	SIL1*	5,0	118,2	510	x			205	22
	TAW2*	4,4	117,9	600	x			184	24
	TAW3*	4,4	117,9	234			x	77	23
	TU	5,5	116,5	10		x		116	20
Flores	BAJ2*	-8,7	121,0	750			x	81	20
	BAJ3*	-8,9	121,0	770		x		122	20
	KEL1*	-8,7	121,9	820			x	121	21
Lombok	LOM1	-8,3	116,4			x		29	14
Luzon	PHI18	15,6	120,1	110				22	14
	PHI20	15,5	121	150				23	7
Negros	PHI1	10,4	123,0					36	11
New Guinea	IJ2	-3,4	135,5	740		x		23	13
	IJ3	-2,6	140,5	200			x	39	16
	PAV	-4,1	139,0	1880		x		207	18
	PNG1	-7,4	146,2	1500				22	10
	PNG3	-7,9	147,1	700				40	17
	UBR	-3,7	140,8	300		x		149	28
Seram	SERA1	-2,8	129,5	50		x		44	6
	SERA13	-3,1	129,5	2600	x			143	10
	SERA16	-3	129,5	650			x	73	11
	SERA17	-3	129,5	650			x	165	12
	SERA23	-2,8	129,5	75	x			28	4
	SERA3	-2,8	129,5	70	x			31	7
	SERA4	-3	129,5	250		x		62	14
	SERA5	-3	129,5	570	x			22	8
	SERA6	-3	129,5	900	x			34	9
	SERA8	-3	129,5	850		x		25	8
	SERA9	-3,1	129,5	1000		x		23	6
Sulawesi	SUL11	0,5	123,5	664	x			36	13
	SUL15	0,5	123,5	1040	x			26	9
	SUL16	0,5	123,5	211			x	24	6
	SUL2	0,5	123,5	211		x		35	11
	SUL7	0,5	123,5	492	x			26	13
Taiwan	TA1	23,1	120,8	1600				41	6
	TA19	24,1	121,8	600			x	64	19
	TA9	24,0	121,2					20	10
Pen. Mal.	GEN1*	3,4	101,8	600		x		37	18
	KED	6	100,5					185	24
	PAS	3	101,5		x			62	13
Vietnam	HOA	22,5	103,5		x			3223	67
Σ (Borneo only)		57 sites			31	16	10	12333	77
Σ (all)		93 sites			41	27	17	17676	159

Appendix II: New or rare regional records of Sphingidae species from own sampling (J. Beck). See Beck & Kitching (2004) for maps with all known records (incl. some unpublished samples) for the species. See Appendix I for site acronyms.

Species	Site (Island)	Comment
Agrius luctifera	KEL1, BAJ3 (Flores)	First record on eastern Lesser Sunda Islands
Ambulyx pryeri	KEL1, BAJ3 (Flores)	Easternmost records
Amplypterus panopus	KEL1 (Flores)	First record on Lesser Sunda Islands
Angonyx testacea	Lembata	First record on eastern Lesser Sunda Islands
Cechenena helops	BAJ3 (Flores)	First record on Lesser Sunda Islands
Gnathotlibus eras	KEL1, BAJ2 (Flores)	First record on Flores, expected
Hippotion boerhaviae	KEL1, BAJ2, 3 (Flores)	First doubtless record on Flores, expected
Hippotion celerio	KEL1, BAJ2 (Flores)	First record on Flores, expected
Hippotion rafflesii	POR8 (Borneo)	First record on Borneo; possibly not uncommon, but easily confused with *H. rosetta & H. boerhaviae*.
Hippotion rosetta	KEL1, BAJ2, 3 (Flores)	First record on Flores since 1909
Hippotion velox	KEL1 (Flores)	First record on Flores, expected
Macroglossum corythus	BAJ3 (Flores)	First record on Flores since 1896
Macroglossum ungues	KEL1 (Flores)	First record on Flores
Marumba cristata	KEL1, BAJ2, 3 (Flores)	First record on the Lesser Sunda Islands
Theretra alecto	BAJ2 (Flores)	First record on Flores, expected
Theretra clotho	KEL1, BAJ2, 3 (Flores)	First record on Flores, expected
Theretra incarnata	Lembata	First record on Lembata, expected
Theretra latreillii	Adonara, Lembata	First records on Adonara & Lembata, expected
Theretra nessus	Adonara, Lembata	First records on Adonara & Lembata, expected
Theretra rhesus	KEL1, BAJ2 (Flores)	First record on Flores

Furthermore, the following interesting specimens were found in the collection of Henk van Mastrigt from Jayapura (all collected in Papua, Indonesia): *Hippotion joiceyi* (first lowland/coastal record), *Hippotion echeclus* (the only confirmed record east of Sumbawa/Sulawesi/Mindanao; a further specimen at the Carnegie Museum (Pittsburgh) from Papua New Guinea was considered mislabelled until this specimen was known); *Cypa* sp., a yet undescribed species.