Wallace's line revisited: has vicariance or dispersal shaped the distribution of Malesian hawkmoths (Lepidoptera: Sphingidae)?

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Large-scale biogeographical patterns of Sphingidae in the Malesian archipelago are investigated, using Geographic Information System-supported estimates of species ranges determined from a compilation of specimen-label databases. Distribution maps for all species and checklists for 114 islands are presented at http://www.sphingidae-sea.biozentrum.uni-wuerzburg.de. Phenetic analyses of island faunas reveal 'textbook'-like patterns of biogeographical associations in the region, with Wallace's line emerging as the main faunal discontinuity in the region. Further analyses, using partial Mantel statistics, indicate that historical features of geography (such as land bridges formed during periods of lower sea levels) are an important determinant of faunal similarity, but recent dispersal can also explain a significant portion of present day hawkmoth distributions. Faunal turnover in relation to distance between islands is steeper for Smerinthinae than for other subfamilies, indicating different dispersal abilities among higher taxonomic groups. These differences are discussed in the light of life-history differences between the subfamilies. © 2006 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2006, **89**, 455–468.

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INTRODUCTION

The Malesian archipelago has been an area of intense biogeographical analysis since A. R. Wallace (1869) first realized the influence of geological history on the distributions of animal and plant species (for recent examples, see Hall & Holloway, 1998; Holloway, 2003). Lowered water levels during long periods in the Pleistocene (Voris, 2000), climate changes (Morley & Flenley, 1987) and tectonic movements (Hall, 1998) have all been suggested to be responsible for the observed large-scale faunal and floral discontinuities, such as Wallace's line (see maps in Monk, de Frete & Reksodiharjo-Lilley, 1997), as well as finer-grained patterns within islands (Musser, 1987; Gathorne-Hardy *et al.*, 2002). An overview over established patterns, including a thorough treatment of the Lepidoptera in the region, can be found in Whitmore (1981, 1987) and Hall & Holloway (1998). However, dispersal, extinction and speciation add stochasticity to data (Ward & Thornton, 2000) and blur the 'geological signal' in species distributions, thus challenging both the understanding of patterns, as well as the application of suitable analytical methods (Holloway, 1998, 2003).

Modern biogeographical analyses investigate regional relationships based on phylogenetic relatedness between taxa (Avise, 2000; van Welzen, Turner & Hovenkamp, 2003), leading to information on dispersal and speciation events that is often neglected in community ecology and biodiversity research (Wiens & Donoghue, 2004). Cladistic methods (Humphries & Parenti, 1999) produce patterns of relationship among areas of endemism that describe the evolutionary history of biotas. However, a number of factors make a cladistic approach difficult in the south-east Asian region even with a robust phylogenetic hypothesis for

the groups under investigation. Due to the geological and geographical complexity of the region, it is difficult to represent hypotheses of geological evolution as a tree structure (Holloway, 1998, 1982; Metcalfe, 1998). Furthermore, a high degree of sympatry, caused by many relatively widespread species, leads to a large number of possible cladograms of regional relationships (Holloway, 1998).

Less rigorous, but not necessarily less precise, than cladistic methods under conditions of insufficient data (Holloway, 1998) are phenetic analyses, in which regions are ordinated according to overall similarities of their faunas. These methods are commonly employed in community ecology (Southwood & Henderson, 2000) and do not require knowledge of phylogeny. Phenetic methods might be precursors to cladistic analytical methods (Baker *et al*., 1998) and are still applied successfully to test geological hypotheses (de Jong, 1998; Kitching *et al*., 2004; but see also Hausdorf & Henning, 2003).

Holloway (1987) identified faunal regions for Malesian Lepidoptera that reflect aspects of the geological history of the region, but also show a strong component from modern-day geography, indicating the importance of dispersal (Holloway, 1998). Based on a phenetic analysis of butterflies and some moth taxa, 'Wallacea' (which comprises Sulawesi and the Philippines except for Palawan) 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. The Lesser Sunda Islands were loosely associated with Sundaland. The fauna of Sulawesi was shaped mostly by dispersal rather than by vicariance of a larger land unit (Holloway, 1997) and appears pivotal to understanding the Lepidoptera patterns in the region. Endemism on Sulawesi is high and biogeographical relations can be found with the Philippines, the Moluccas, and the Lesser Sunda Islands, depending on the taxon and the habitat (i.e. altitudinal zone) under investigation (Holloway, 1997), yet similarity to nearby Borneo is relatively low (Holloway, 1998).

In the Malesian region (defined here as the area between the Andamans, Sumatra and Peninsular Malaysia, through Indonesia, the Philippines and Papua New Guinea, to the Solomon Islands; see also Figure 2; Beck & Kitching, 2004), 310 Sphingidae species are known, which is approximately 20% of the global species richness for this family (Kitching & Cadiou, 2000). Sphingid moths are among the few tropical insect taxa for which large-scale analyses of biogeography and macroecology can be attempted with sufficient confidence in data quality because not only a long-standing scientific effort, but also two centuries of data from hobby collectors and Lepidoptera enthusiasts have contributed to a decent knowledge of their taxonomy and general biology (Kitching & Cadiou, 2000; Holloway, Kibby & Peggie, 2001). Details on their distribution in Asia can be found in Pittaway & Kitching (2003) and Beck & Kitching (2004).

The present analysis explores the following questions:

1. Do Sphingidae show similar patterns of faunal similarity to those previously established for other Lepidoptera (as described by Holloway, 1987)?
2. To what degree can the observed patterns be explained by known patterns of geological and geographical history?
3. How do patterns of faunal similarity and species turnover differ among taxonomic subgroups of Sphingidae, and what conclusions can be drawn from such differences?

MATERIAL AND METHODS

COMPILATION OF RECORDS

From the published literature, unpublished species lists, museum, and private collections, the global distributions for all hawkmoth species from South East Asia (including New Guinea and the Solomon Islands) were compiled from more than 35 000 records. A complete literature listing, together with details of unpublished data sources, can be found in Beck & Kitching (2004). Much effort was expended to minimize error possibilities (Graham *et al*., 2004) by checking data for taxonomic inconsistencies (following Kitching & Cadiou, 2000; more recently published taxonomic literature) and by identifying the correct locations of sampling sites. Latitude and longitude could be assigned to most records with an accuracy of at least 1° (giving a maximum error of approximately ±80 km near the equator).

ESTIMATING RANGE AREAS

Records were entered into a Geographic Information System (GIS; ArcView, 2000) in which it was possible to display them by species, subspecies, record accuracy, altitude or year of sampling (if known). A number of GIS-compatible habitat maps were used to underlay the species records to find patterns of distribution. Altitudinal relief, vegetation zones, precipitation, and minimum winter temperature often matched the outer limit of a species' records, and a number of apparently important parameters limiting sphingid distributions could be identified (Quinn, Gaston & Roy, 1997, 1998; Cowley *et al*., 2000). The limits of many species within Malesia, however, appear to be determined more by recent or historical geography than by habitat alone and, in that region, species ranges were not extended beyond the actual records. Generally, a conservative approach was adopted that

would underestimate rather than overestimate species' ranges. Subspecies divisions often yielded important clues as to whether a gap in a distribution indicated a genuinely disjunct range or was just a result of undersampling. Uneven sampling effort in different parts of the region disturbs this straightforward procedure (Graham *et al*., 2004; Fagan & Kareiva, 1997; Soberón, Llorente & Oñate, 2000). A species that is unrecorded in relatively well-sampled northern Thailand or north-east Borneo is much more likely to be genuinely absent from that area than it is in the much more poorly sampled areas of southern (Indonesian) Borneo or the northern Moluccas. Furthermore, certain species (e.g. those not strongly attracted to light) are more likely to be overlooked than others. In addition, misidentifications by nonspecialists are much more likely in some genera (e.g. *Macroglossum*) than others.

Taking all these factors into consideration, the best possible estimate of each species' range was digitized. Checklists of recorded species and estimated faunal composition could be extracted from these data for 114 islands of the Malesian archipelago. All range maps and island checklists, as well as an example of the process of range estimation, are given in Beck & Kitching (2004); for details, see also Beck (2005).

Similar approaches to estimating Lepidoptera species ranges have been used previously in both computerized (Cowley *et al*., 2000) and noncomputerized (Hausmann, 2000) form. However, no explicit computer model was used in the present study to estimate ranges. Computer models have been successfully used for range estimates on smaller geographical scales (Ray, Lehmann & Joly, 2002; Raxworthy *et al*., 2003; Iverson & Prasad, 1998) and would be desirable for their rapid application to a large number of species. However, the analysis of presence-only data, which is typical of museum data (Graham *et al*., 2004), is still problematic for statistical habitat models (Cowley *et al*., 2000; Zaniewski, Lehmann & Overton, 2002). Despite the apparent 'subjectivity' of the approach that was chosen in the present study, a noncomputerized approach is still probably more precise due to its easier consideration of species differences, be they ecological requirements, if known, or recording constraints.

ANALYSES OF FAUNAL SIMILARITY

Checklists for islands were used for phenetic analyses of biogeographical patterns, ignoring faunal patterns that occur within some islands. Only analyses of estimated data on island faunas are presented here, which yielded clear and readily interpretable results. Recorded data did not perform well, presumably due to strong effects of undersampling of faunas on all but the largest islands of the archipelago, although lower-order clustering often matched that of estimated data (for data, see Beck & Kitching, 2004).

As a first step, nested island faunas (i.e. faunas that are completely contained within some other, typically nearby and larger island) were identified (based on estimated data) and excluded from some analyses because they could disturb clustering and ordination processes due to nonmetric arrays of similarity coefficients (Holloway, 2003). Of the 114 islands for which data were available, 38 non-nested island faunas remained for further analyses. Preston's coefficient of faunal resemblance (Preston, 1962) was used in combination with single-linkage cluster analysis (Holloway, 2003). Preston's coefficient is derived from principles of the species-area relationship (Rosenzweig, 1995) and has some interesting properties for biogeographical analysis: If z, which measures the relative faunal distance between two samples from 0 to 1, 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). However, if $z > 0.27$, then 'there is, and has long been, some degree of genuine isolation' (Preston, 1962). Coefficients were calculated according to the table in Preston (1962: 419). Because the results of clustering and ordination analyses are often heavily dependent on the method employed (Hengeveld, 1990; Southwood & Henderson, 2000; Holloway, 2003), several other approaches were also used to corroborate the resulting patterns. The results of nonmetric multi-dimensional scaling (Legendre & Legendre, 1998) of Sørensen-indices, cluster analyses based on Bray–Curtis coefficients (Southwood & Henderson, 2000), as well as a table of the Preston coefficients, can be found in Beck & Kitching (2004). There is generally great controversy on the calculation of similarity or β-diversity (Koleff, Gaston & Lennon, 2003), and no single measurement or index can perfectly capture all aspects of this concept. Cluster analyses and other ordination techniques were calculated using software provided by Statsoft (2003) and Henderson & Seaby (2002).

Observed patterns of similarity were tested for statistically significant groupings by conducting permutation tests for several hypothetical faunal boundaries in an analysis of similarities (ANOSIM, 10 000 randomizations of the Preston-similarity matrix), using the computer program Primer 5, 2002).

The influence of distance and land-units during lower sea levels was analysed with partial Mantel tests (Legendre, 1993; Legendre & Legendre, 1998; Bohonak, 2002) that were applied to matrices of faunal similarity (1 – Preston coefficients) for the non-nested islands. Geographical distances between island centroids were calculated from latitude and longitude data (using geodesic correction; ArcView, 2000). As a

second predictor, a binary matrix for unified land areas during lower sea levels was assembled from both the 50-m and 100-m contour maps in Voris (2000). During the last 17 000 years, sea levels in South East Asia dropped for 7000 years as low as or lower than 50 m and, for 4000 years, as low as or lower than 100 m below the present day coastline (Voris, 2000). The Bismarck and Solomon Islands were not included in the maps of Voris (2000), and thus only 31 island faunas could be tested.

RESULTS

PHENETIC CLASSIFICATION OF REGIONS

A classification of islands by faunal similarity is shown in Figure 1, with a linkage diagram for the same data shown in Figure 2. The dendrogram yields clear and interpretable patterns. Wallace's line appears as the main faunal discontinuity in the region. Only the Tanimbar Islands do not fit this 'clas-

sical' pattern, being associated with the western, instead of the eastern, part of the archipelago, and in particular with the Lesser Sunda Islands. The western subregion falls into four main blocks: (1) the Sundaland area (except Palawan) clusters together, with Java slightly separate from the other main islands; the Sundaland islands share a high biological similarity in many groups of organisms (Whitmore, 1981, 1987) because they formed a continuous landmass during times of lower sea levels (Voris, 2000); (2) the main Philippine islands group closely together, but Palawan, which is grouped with Sundaland for many other taxa (Whitmore, 1987), is only loosely associated with them; (3) the 'Sulu archipelago' (Jolo, Tawitawi) in the south-eastern Philippines has a quite distinct fauna that is well separated from that of the rest of the Philippines, Borneo or Sulawesi; and (4) the Lesser Sunda Islands form a tight block within the western subregion (see also Holloway, 1987), but the Andaman Islands are very isolated and only loosely associated
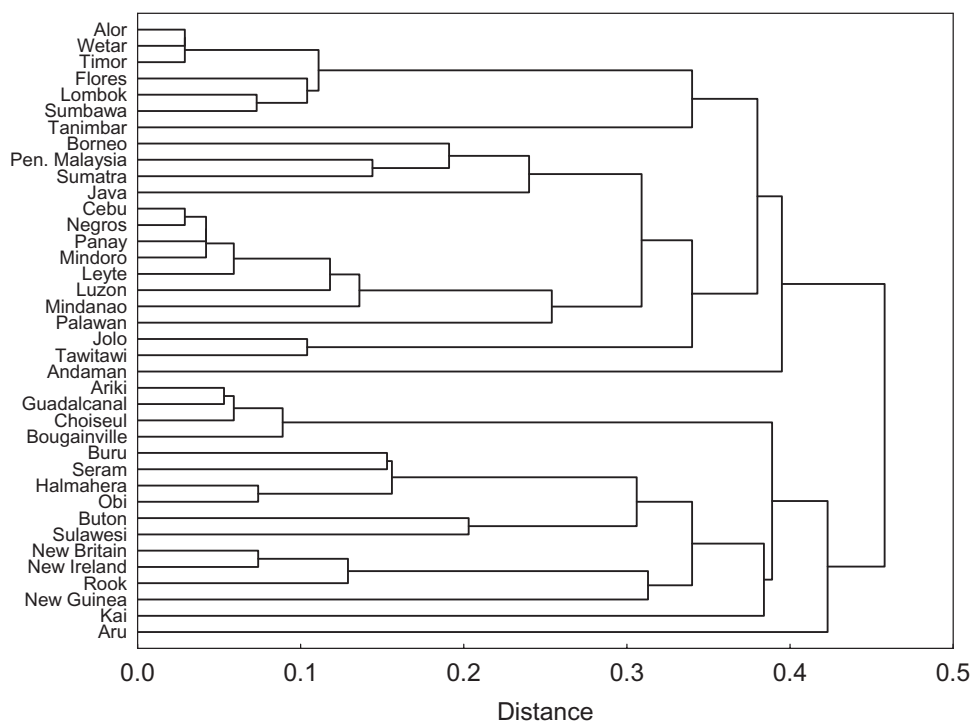
Figure 1. Biogeographical associations of Sphingidae in the Malesian archipelago (single-linkage cluster analysis for 38 islands, based on Preston's coefficient; Preston, 1962). The listed islands have nested faunas (i.e. they are fully contained, as inidcated in italics) and were excluded from analysis (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, Homonhon, 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, Fergusson, 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, Simeuluë, Pagai-Pagai, Pini, Mentawi. *Sumbawa*: Sumba, Komodo. *Tanimbar*: Yamdena, Selaru, Larat ('Tanimbar islands'). *Timor*: Damar, Leti, Roma, Sermatta ('Bandar Daya islands').
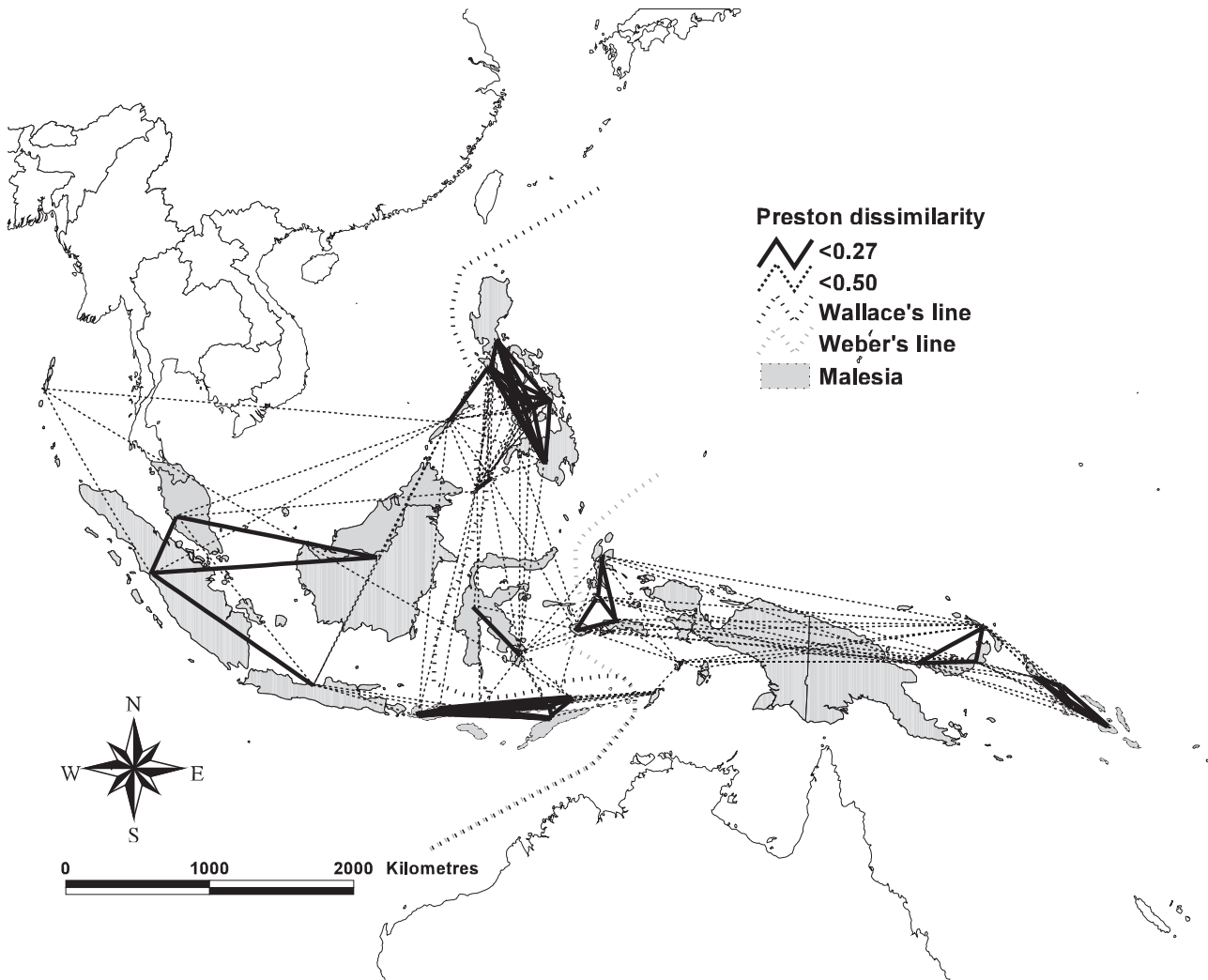
Figure 2. Linkage diagram of Sphingidae faunas based on Preston's coefficient. For easier geographical association, islands in the diagram are displayed on their geographical position in a map of South East Asia (projection: sinusoidal). Preston coefficients > 0.27 indicate isolation between regions (see methods).

with the rest of the archipelago. In the eastern subregion: (1) the Solomon Islands (including Bougainville) are a clearly separate archipelago, as are (2) the Bismarck Islands. New Guinea appears to have quite an isolated fauna, which is probably caused by a high number of endemics (Table 1); (3) the Moluccas (except of the southern island groups of Aru, Tanimbar and Kai) form a block that divides into a northern and a southern part, whereas (4) Sulawesi is closely associated only with Buton. By contrast to the assessment by Holloway (1987) (based on phenetic analyses as well as area-cladograms from allopatric species arrays), 'Wallacea' and 'Melanesia' appear as quite heterogeneous regions for Sphingidae. The geographically isolated Kai and Aru islands, similar to the 'nearby' Tanimbar Islands, have relatively isolated faunas within their subregion, but only on the latter

island group are endemic hawkmoth species known (Table 1).

A comparison with a cluster analysis based on Bray–Curtis similarities (data not shown, see 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 subregion, indicating that these islands are a transition zone between east and west. Similarly, Palawan is grouped with Sundaland rather than the main Philippines group, thus also showing the transitional character of this island's fauna. An analysis of Sørensen indices in combination with multi-dimensional scaling (data not shown, see Beck & Kitching, 2004) confirms this judgement. The suggestion that Weber's line (between Sulawesi and the Moluccas; Monk *et al.*, 1997) is the main faunal discontinuity for hawkmoths

Table 1. Degrees of endemism in the major regions as well as selected islands of the Malesian archipelago

Region	Endemics*	Species (total)	% Endemics
Andaman	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 Lesser Sunda (NTB)	2	51	3.9
Easter Lesser Sunda (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 that are not found in other parts of the Archipelago, but many range into continental South East Asia.

in the region (as for some other Lepidoptera groups; Holloway, 1987) is not supported by these data.

ANOSIM reveals significant effects of: (1) Wallace's line ($R_{global} = 0.681$, $P < 0.001$); (2) regions according to Holloway (1987) (Sundaland, Wallacea, Lesser Sunda Islands, Melanesia: $R_{global} = 0.625$, $P < 0.001$, all pairwise comparisons significant); and (3) a grouping according to Figure 1 at a distance of $z = 0.27$ (see also Fig. 2: $R_{global} = 0.987$, $P < 0.001$). In the last test, some nonsignificant pairwise comparisons occur, but relate to groups with only one or few islands, and hence to comparisons with low statistical power. Interesting pairwise test results are a clear separation within

'Wallacea' (Sulawesi-group : Philippine-group, Philippine-group : Sulu archipelago, both $P = 0.022$).

Table 1 gives figures for the degree of species endemism of the main regions and some selected islands. A relatively high degree of endemism justifies the separation of all major regions from each other. However, endemism of some islands or island groups within major regions indicates a high degree of isolation. Particularly, 22% endemic species in Sulawesi make a grouping with the Philippines as 'Wallacea' questionable. However, sphingid taxonomists do tend to separate populations from the Philippines and Sulawesi into pairs of 'good', albeit very similar species (e.g. *Daphnis hayesi* Cadiou/*Daphnis vriesi* Hogenes & Treadaway), which might be partly responsible for this effect.

Separate cluster analyses of the subfamilies (based on Bray–Curtis coefficients for easier computation) mostly show the same patterns as those found for the family as a whole as far as subgroups of similar islands are concerned (Fig. 3). However, the interrelationships of these subgroups differ between subfamilies, and in the Smerinthinae in particular distance measures between subgroups are considerably larger than for other subfamilies. For Smerinthinae, Lydekker's line between the Moluccas and New Guinea (Monk *et al*., 1997) appears as the major faunal discontinuity in the region (of the tribe Smerinthini, only two species of *Cypa* are confirmed from east of Lydekker's line). Also noteworthy is the huge separation between the Solomon Islands and the rest of the archipelago in the Sphinginae, a pattern that was not observed for other subfamilies.

CORRELATES OF FAUNAL SIMILARITY: MODERN-DAY DISTANCE OR ANCIENT LAND BLOCKS?

A Mantel test shows that both geographical distance and unified land areas during periods of lower sea levels correlate significantly with faunal similarity, independently as well as in partial tests (Table 2). The logarithm of geographical distance alone is a significant predictor of variation in faunal similarity and does not lose much explanatory power in a partial analysis (controlled for blocks of historically unified land masses). Land unity also has a significant effect (in univariate as well as in partial analysis), but r-values are lower than for geographical distance. However, the latter statement might not be relevant because the binary data structure is much coarser than that for distance. The same analyses were also performed for the two larger subfamilies

Figure 3. Biogeographical associations of the three subfamilies of hawkmoths in Malesia (Bray–Curtis similarities, single linkage cluster).
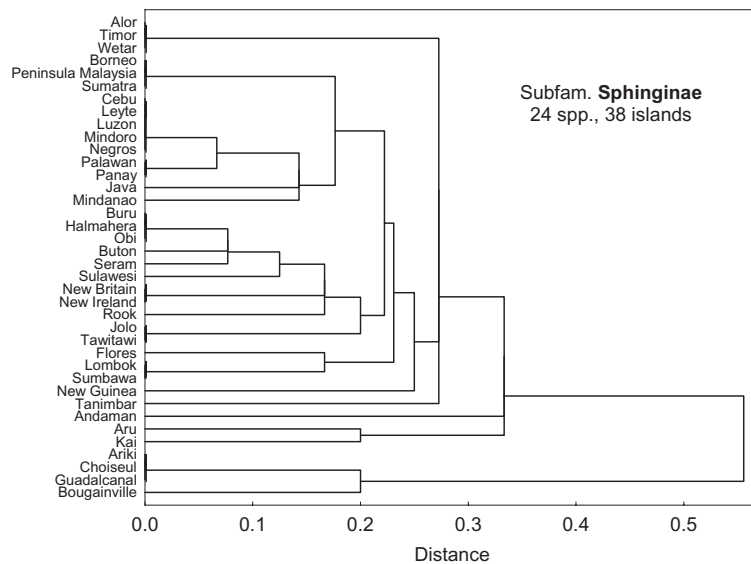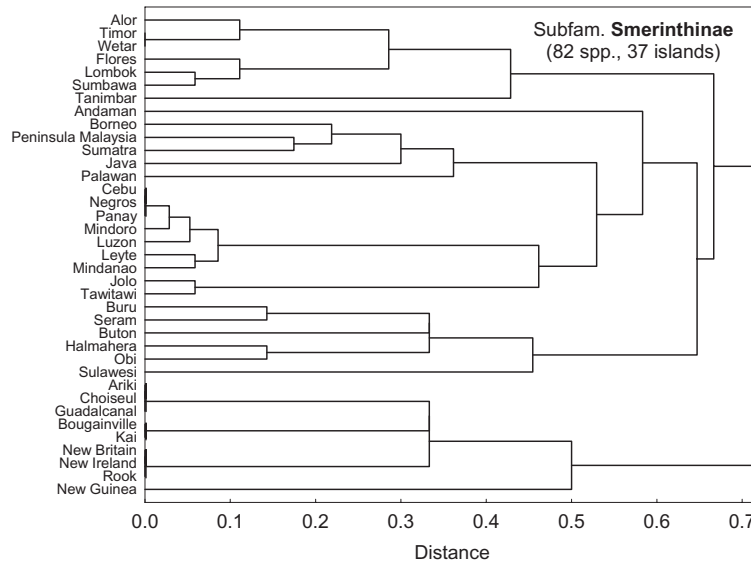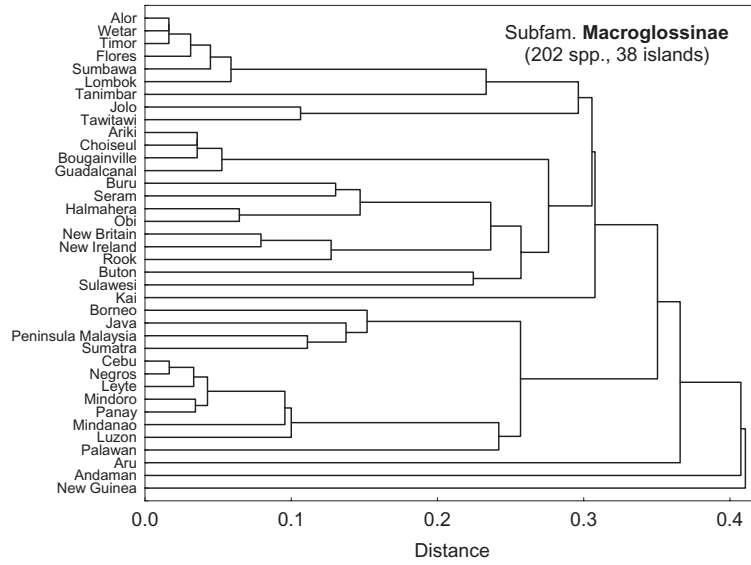
Table 2. Test results from partial Mantel-tests of 31 faunal similarities with geographical distance and land-units at sea levels 50 m and 100 m below present (Bohonak, 2002; 10 000 randomizations)

Correlation of faunal similarity	50-m contour		100-m contour	
	Z	r	Z	r
Log_{10}(geographic distance) (m)	1530.5	0.773	1530.5	0.773
Land unity (binary code)	241.7	0.571	228.5	0.546
Log_{10}(geographic distance), partial		0.720		0.714 (controlled for land unity)
Land unity, partial		0.439		0.381 (controlled for geographic distance)

All tests are significant at $P < 0.0001$.

(Macroglossinae, Smerinthinae) separately. The results indicate a stronger influence of geographical history on the distribution of the Smerinthinae [50-m contour: log_{10}(geographic distance), $r_{partial} = 0.498$; land unity, $r_{partial} = 0.485$] than on those of the Macroglossinae [log_{10}(geographic distance), $r_{partial} = 0.695$; land unity, $r_{partial} = 0.337$]. Nevertheless, all partial Mantel correlations are highly significant for both taxa ($P < 0.0001$).

SIMILARITY AND FAUNAL TURNOVER OF SUBFAMILIES

Figure 4 demonstrates faunal similarity as a function of distance between islands (but ignoring all other biogeographical effects). This is presented as an alternative analysis to the Mantel tests reported above. The use of Sørensen indices (which are much faster to calculate than Preston coefficients) allowed an analysis of all 114 islands, as well as a taxonomic splitting of data down to tribe level where this seemed appropriate (see below). Nonparametric, Mantel-type permutation tests were used to establish the significance of the relationship between geographical distance of islands and β-diversity of the family Sphingidae as a whole, as well as the three subfamilies and the two larger tribes of the subfamily Smerinthinae (Table 3). Distance emerges as a key predictor of faunal similarity (confirming the results reported above), and there are clear differences in the slope of the relationship. Smerinthinae faunal similarities are much more (negatively) strongly influenced by distance than are those of Macroglossinae or Sphinginae, indicating inferior dispersal ability in the former group. The slope of the relationship between the two major tribes of Smerinthinae, however, does not differ. Ambulycini do not show a flatter but steeper slope than Smerinthini (see below for relevance and discussion). The latter group shows a considerably weaker distance-turnover relationship (lower R-value), which indicates that factors other than present day geographical distance (e.g. ancient coastlines, see above) have been more influential in shaping the distribution of this group.

Table 3. Significance of the relationships shown in Figure 4 is confirmed by a nonparametric randomization test (RELATE, using PRIMER 5, 2002; 10 000 randomizations)

|	Rho (Spearman's R, corrected for tied ranks)	N (occupied islands)
Sphingidae	0.688	114
Macroglossinae	0.704	114
Sphinginae	0.601	111
Smerinthinae	0.665	108
Ambulycini	0.708	102
Smerinthini	0.466	80

RELATE produces Mantel-type test results without any assumptions regarding data distribution or linearity of the relation. All tests are significant at $P < 0.0001$.

DISCUSSION

BIASES AND CIRCULARITIES IN RANGE ESTIMATES

Estimating species ranges from recorded data is an essential prerequisite for almost all larger-scale analyses of distribution patterns. Leaving aside the very few really well sampled organisms (e.g. European and North American birds), geographical ranges of most organisms 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 measurements of species in 100-km^2 grid cells are an option for British butterflies (Quinn, Gaston & Arnold, 1996), but not for those in New Guinea. Such differences can strongly influence methods and results of analyses (Bolliger, Sprott & Mladenoff, 2003; Graham *et al*., 2004). GIS modelling is an increasingly powerful aid to making distribution estimates more reliable and fine-grained (Guisan, Edwards & Hastie, 2002; Segurado & Araujo, 2004). However, a model can only be as good as its underlying assumptions and the quality of reference data.
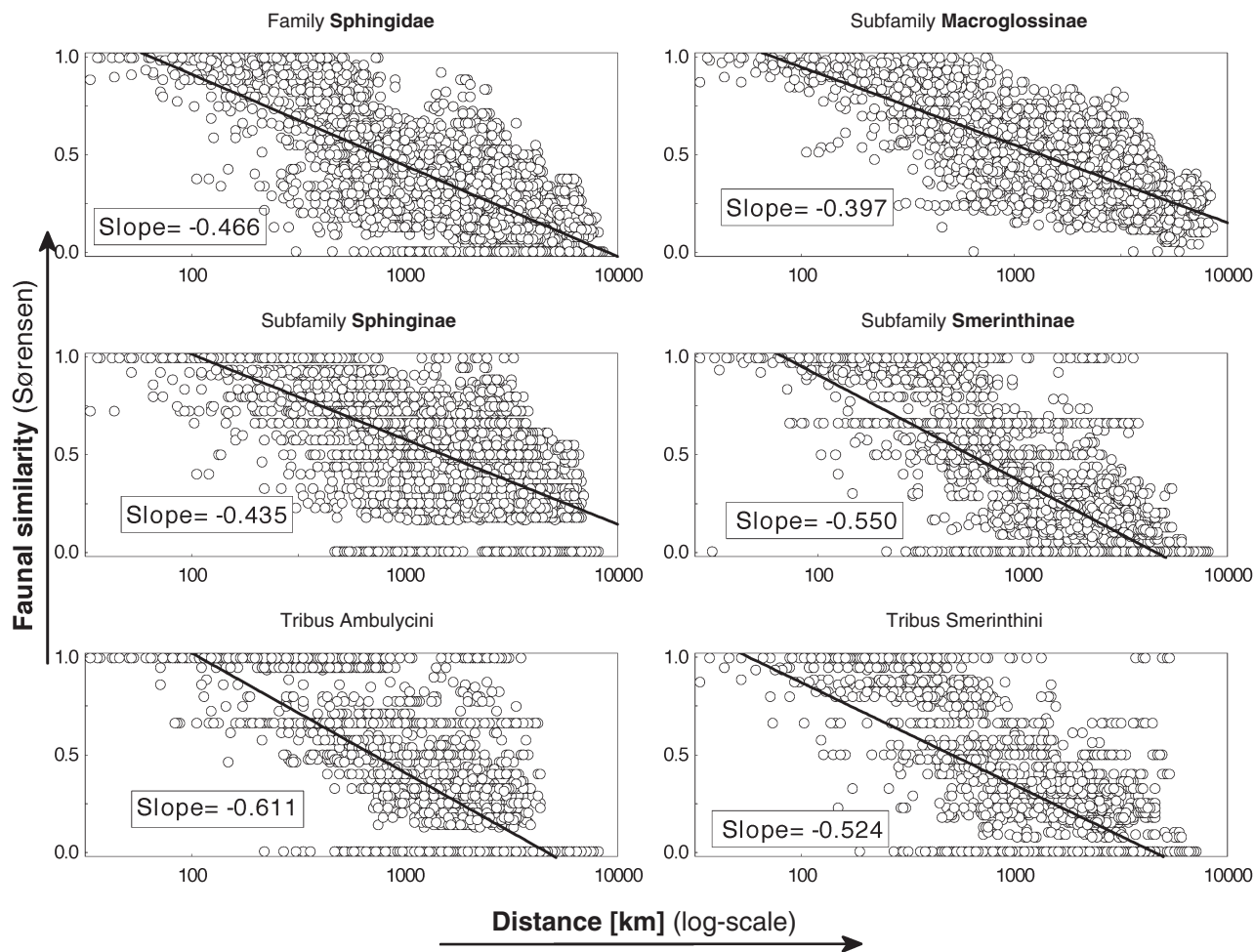
Figure 4. Faunal similarity (based on Sørensen indices) of estimated island faunas in relation to distance between islands for all Sphingidae (upper left graph) and the three subfamilies separately. Statistical tests cannot strictly be applied because sample sizes are inflated with non-independent data in this representation, although a comparison of regression slopes of the Sphingidae and the three subfamilies is still meaningful as the data refer (almost) to the same islands; therefore, the sample size inflation is equal in all graphs (Table 3).

Irrespective of whether a computerized algorithm (Raxworthy *et al.*, 2003) or a 'human controlled' approach (the present study) is used to infer the assumptions on species ranges, artefacts in distribution patterns can be created that might cause circularity: assumptions about distribution patterns will be proven in the subsequent data analysis. Because recorded data are not a reasonable option for tropical invertebrates due to obvious undersampling effects, potentially biased results must be accepted yet carefully discussed and, if possible, confirmed by independent analyses to be interpreted correctly.

Topographical 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 reported in the present study. Although our estimated distributions did not normally cross the boundaries of geographically tightly-clustered island groups without evidence from positive records, two assumptions may have led to artefacts. First, whereas species with restricted range records were treated very conservatively, this was not carried out for a few very widespread species with dense records in all well-sampled regions. By contrast, it was assumed that such species had high dispersal abilities [and sometimes pan-tropical distributions, e.g. *Agrius convolvuli* (L.)] and would have reached even relatively remote, undersampled regions and particularly small islands near to 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 by taxonomists and hobby collectors because they are 'nothing special'

(Graham *et al*., 2004). Second, geographically dense archipelagos were often treated as one 'unit', where a positive record on some islands was taken to indicate occurrence on all islands. This applied particularly to badly sampled islands and to species that are difficult to find (e.g. because they do not come to artificial light sources) or which are easily misidentified or confused with a commonly reported species. Specifically, the high faunal similarity of the central Philippines and of the Solomon Islands might have been artificially inflated by this procedure.

IS SPHINGID 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 (Whitmore, 1987; Hall & Holloway, 1998; for other regions, see also Jansson, 2003) and could also be observed for Sphingidae in the present study. Patterns such as the unity of Sundaland and the central Philippine islands, as well as their connection through transitional Palawan, or the similarity of Sulawesi and New Guinea to their surrounding islands, can be readily explained by lower sea levels (Voris, 2000), which unified these areas but left deep sea zones, as well as unsuitable habitat due to climatic differences, between them (Brandon-Jones, 1998; Gathorne-Hardy *et al*., 2002; see also vegetation maps in Pickett *et al*., 2004). Subsequent rises in sea level caused vicariance within the land blocks and led to ordered extinctions on the smaller islands (Atmar & Patterson, 1993), which were disturbed by random events. Other island groups, however, do not share such a history. For example, the Moluccas is a geologically diverse region that has never formed a single, connected block of land (Hall, 1998; Metcalfe, 1998). Consequently, different distribution patterns and a generally higher heterogeneity than within island groups such as Sundaland should be expected within the Moluccan region (e.g. for butterflies, see de Jong, 1998), if geological history was the major determinant of species distribution.

However, sphingid faunas in regions with a homogeneous history such as Sundaland do not have a higher similarity than those of the 'composite' archipelago of the Moluccas (Fig. 1; mean ± SD Preston coefficient: Sundaland, 0.25 ± 0.08; Moluccas, 0.26 ± 0.18). Furthermore, a nestedness analysis of matrix temperatures (Atmar & Patterson, 1993, 1995; Beck, 2005) also indicated no differences in species distributions between geologically homogeneous and heterogeneous regions.

Although a geological basis is still clearly present in sphingid distributions (Fig. 2) and patterns of endemism (Table 1), the above results lead to the conclusion that dispersal has influenced the island groups so heavily that differences between regions of sea-level induced vicariance and areas of genuine geological heterogeneity are blurred beyond recognition.

Partial Mantel tests were used to confirm that both distance and land unity have a significant influence on sphingid distributions. Sea level maps at 50 m below current levels are better predictors of faunal similarity than those for 100 m. However, it remains unclear in what time-frame the distribution of hawkmoths over South East Asia developed. It must be expected that different phylogenetic lineages might have dispersed and speciated at very different times, and thus under different geographical conditions. For example, this might be reflected in the different biogeographical patterns of the three subfamilies (Fig. 3). With a possible Miocene origin of the family (Zhang, Sun & Zhang, 1994), some Sphingidae lineages at least must have been present in South East Asia for a much longer time period than the most recent, late Pleistocene changes in climate and sea-level, which complicates considerably our understanding of what caused present day distribution patterns. A cladistic analysis of the biogeographical patterns of Sphingidae lineages of different evolutionary age, as well as comparisons to other Lepidoptera (such as Saturniidae), might help to answer such questions, but, as a first step, would require a reasonable phylogenetic hypothesis for these taxa (Barraclough & Vogler, 2000).

Most Sphingidae are accomplished fliers with migratory tendencies in some taxa. Furthermore, many Macroglossinae species at least appear not to be bound to ecologically stable, undisturbed habitats in South East Asia (Beck, Kitching & Linsenmair, 2006a). These factors make it likely that many sphingids are extraordinarily good dispersers, and some species have very large ranges (Beck, Kitching & Linsenmair, 2006b). Lack of distribution data of similar quality make it difficult to compare sphingid range sizes with those of other Lepidoptera groups in South East Asia, but a comparison of European distributions (from country lists in Karsholt & Razowski, 1996; multiplied by summed country area) shows much larger European ranges for Sphingidae than for Papilionoidea, Geometridae, Noctuidae or Lepidoptera as a whole (Kruskal–Wallis analysis of variance, $N = 8459$, $H = 78.6$, d.f. = 4, $P < 0.0001$). Thus, it is unsurprising that dispersal between islands occurs regularly and plays an important role in sphingid distribution in the Malesian region (for a general discussion of long distance dispersal in Lepidoptera, see also Ferguson, 1991).

The effect of these dispersal abilities becomes evident in comparison with very poorly dispersing insect groups. Distribution patterns of Malesian cica-

das, for example, are heavily influenced by geological history and still represent historic rather than present geography (de Boer & Duffels, 1996). In water bugs (Heteroptera), interisland dispersal plays a role, although distribution patterns can be related to geological history even within islands (Polhemus & Polhemus, 1990, 1998). The potential effects of undersampling upon results of these studies, however, are unknown.

DISPERSAL AND LIFE-HISTORY STRATEGIES

Differences in dispersal ability are likely to be responsible for differences in the distribution of subfamilies (cf. Hovestadt *et al.*, 2005). It is suggested that these differences are ultimately caused by different life-history strategies, specifically the presence and absence of adult feeding (i.e. income vs. capital breeding) in different groups of the Sphingidae (Lemaire & Minet, 1998), which might also have consequences on their frequencies in local habitats (Beck *et al.*. 2006a) and affects regional patterns of species richness (Beck, Kitching & Linsenmair, 2006c).

Macroglossinae and Sphinginae have a well-developed proboscis for flower feeding, whereas Smerinthinae have a reduced or missing proboscis (Kitching & Cadiou, 2000). The consequences of a capital breeding life history (e.g. reduced longevity, higher morphological, and behavioural dimorphism between the sexes; Janzen, 1984) are proposed as a hypothetical explanation for observed differences in the biogeography of the taxa; Smerinthinae are weaker dispersers than the two other subfamilies, as was shown by the steeper distance-turnover relationship (Fig. 4). Furthermore, partial Mantel correlations indicated a stronger influence of past geography in this group than on the better dispersing Macroglossinae. The dispersal abilities of Smerinthinae are possibly inferior because they cannot reach the islands, due, for example, to the weaker flight abilities of females with heavy egg-loads (which has a negative effect on flight performance, Didley, 1995), or because of a shorter adult life span (see Tammaru & Haukioja, 1996 and references therein). Within the subfamily Smerinthinae, a capital breeding life history is evident in the tribe Smerinthini (Kitching & Cadiou, 2000), but not in the tribe Ambulycini. Species of this latter tribe feed on flowers as adults (as inferred from the presence of pollen on their probosces; J. Beck, unpublished data), but nevertheless show a steep faunal turnover (Fig. 4). Smerinthinae might generally be weaker and less agile fliers than Macroglossinae as concluded from morphological differences (lower average 'wing load'; Beck, 2005). Larval host-plant relationships might also play a role (diet breadth is related to range size; Beck & Kitching, in press) but, in an analysis of available host plant data, no significant differences in diet breadth were found between Smerinthinae and Macroglossinae (Beck *et al.*, 2006d).

Analyses of sphingid species richness of the Melanesian islands (Beck *et al.*, 2006b) lead to an analogous, life history-related interpretation to that outlined above. However, further investigation will be needed to categorize confidently the life-history traits of the tribe Ambulycini, which show the distribution patterns of the capital breeding Smerinthini but an apparently income breeding life history. Furthermore, their systematic position is not unchallenged. Some workers have associated them with the Sphinginae rather than with the Smerinthinae (Nakamura, 1976) on morphological grounds, which would correspond with their suggested life-history association (see above).

Differences in species' abilities to reach and persist on islands were recently put forward as a model to explain patterns of island biogeography (Lomolino, 2000; see also Diamond, 1975), an alternative to McArthur & Wilson's classical equilibrium model (for a review and discussion, see Whittaker, 1998). It remains to be seen whether further analyses of hawkmoth data support predictions from this approach at a species level.

Allopatric speciation is to a large extent dependent on isolation of populations or founder individuals (Mayr, 1963). Therefore, lower dispersal abilities should, all else being equal, lead to higher speciation rates. Speciation patterns were not explicitly addressed in the present study (partly because of the unresolved phylogenies in many groups) but, as a first assessment, the ratio between Smerinthinae to the two other subfamilies of complete (estimated) island faunas and the respective endemic portion could be compared. For three island faunas with a relatively high proportion of endemics (Table 1), contingency tables did not reveal significant differences in proportions (New Guinea: $\chi^2 = 0.30$, d.f. = 1, $P_{one-sided} = 0.292$; Sulawesi: $\chi^2 = 2.39$, d.f. = 1, $P_{one-sided} = 0.061$; Tanimbar: $\chi^2 = 0.35$, d.f. = 1, $P_{one-sided} = 0.277$), although data from Sulawesi show a strong trend towards a higher proportion of Smerinthinae among the endemic species.

The correlations of life-history traits, such as adult resource allocation, (suspected) adult longevity and sexual dimorphism, with patterns of distribution and dispersal (see above, Beck & Kitching, in press), range size (Beck *et al.*, 2006c) and local habitat (Beck *et al.*, 2006a; see also Southwood, 1988) match results of a relation between these variables in other tropical Lepidoptera (Braby, 2002 and references therein; Janzen, 1984), as well as in temperate regions (Brändle, Öhlschlaeger & Brandl, 2002).

CONCLUSION

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

Faunal turnover of islands in relation to distance between islands is steeper for Smerinthinae than for other subfamilies, indicating differences in dispersal ability between taxonomic groups. These differences can be explained hypothetically by differences in adult resource allocation between the taxa (i.e. capital breeding vs. income breeding life histories). However, further studies will have to confirm the ecological reality of these life-history differences, which are to date mainly inferred from taxonomic affiliation and proboscis morphology.

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