Evolutionary Ecology Research, 2006, **8**: 677–690

Extending the study of range–abundance relations to tropical insects: sphingid moths in Southeast Asia

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ABSTRACT

Question: Is there a positive relationship between local abundance and geographic range size in tropical insects? Studies on other taxa have suggested this relationship is a general rule in community ecology.

Data studied: Comprehensive range area measurements from GIS-supported distribution estimates and local abundance measures based on light trapping were available for sphingid moths across Southeast Asia and the Malesian archipelago. Data stem from a combination of our own fieldwork and published and unpublished collections.

Search method: We regressed range area of species on their local commonness within each sample site. We then used meta-analysis to test for an effect across sites, as well as to detect differences between habitat types and regions. We repeated all analyses with independent contrasts to control for potential impacts of phylogeny (using a taxonomic classification as a surrogate for a phylogeny).

Conclusions: Range size is related to local abundance. It would appear that there is an influence of geographical position and habitat disturbance on the strength of the relationship. Correlations of range and abundance with the number of larval host plant families used, as well as other cues for a mechanistic explanation of the range–abundance relationship, are discussed.

Keywords: density, distribution, macroecology, meta-analysis.

INTRODUCTION

A positive relationship between the local abundance and the geographical distribution of species has been documented in so many studies that it is considered one of the general rules of macroecology (Gaston, 1996; Bell, 2001; for a recent case study, see Harcourt *et al.*, 2005). Not only does its broad empirical support make this relationship interesting, but also its potential to provide a link between various large-scale patterns of community organization, such as species

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richness, relative abundance distributions, and the distribution of range and body sizes (Maurer, 1999; Blackburn and Gaston, 2001).

However, despite this, and the importance of the range–abundance relationship (RAR) for applied purposes such as conservation and harvesting (e.g. Warren *et al.*, 2003; Jennings and Blanchard, 2004), research on the RAR still has several shortcomings as a generalizing character of macroecological theory. First, despite the broad taxonomic breadth of investigations, there is a strong bias towards temperate region vertebrates and plants (Gaston, 1996; Maurer, 1999). In particular, tropical insects have rarely been studied, and to our knowledge never on a spatially extensive scale. Hence, research does not reflect the global distribution of biodiversity, which is concentrated among tropical arthropods (e.g. Myers *et al.*, 2000). Second, there are inconsistencies in the measurement of investigated parameters across studies (Gaston, 1996), for example using either comprehensive ranges or simply small fractions of species' actual distributions. Analyses at different scales might measure different phenomena (Blackburn and Gaston, 1998; Stoffels *et al.*, 2003). Furthermore, means of abundance across those sample sites where a species occurs are often used, although in most studies this measure relies on the assumption of fairly uniform spatial distribution of abundance. In reality, however, such distributions can be complex and multi-peaked (Gaston *et al.*, 1997; Brewer and Gaston, 2003). Third, a number of mechanisms have been proposed to be causal for RARs (e.g. Gaston *et al.*, 1997), but largely fail to be rigorously testable on realistic data sets. As an experimental approach is impossible in most life-size ecosystems (but see, for example, Holt *et al.*, 2004), only a detailed documentation of the natural variability of the relationship remains as a means for hypothesis generation and testing. This variability might involve, for example, differences between taxa, lifestyles, habitats or evolutionary age of taxa (e.g. Johnson, 1998).

A spatially extensive analysis of the RAR in the sphingid moths of Southeast Asia and Malesia is presented here. Besides butterflies, this Lepidopteran family is probably the best known of the tropical insect taxa (Kitching and Cadiou, 2000). Meta-analysis is introduced as a powerful tool of analysing RARs, as it not only overcomes some of the problems of local abundance measurement (see above), but also allows exploration of the strength and direction of correlations within *a priori* chosen site categories.

METHODS

Data sources

Geographic distributions of species were estimated from original records in a GIS-supported procedure that is described in detail in Beck and Kitching (2004). In short, we compiled more than 34,500 distribution records from museums, publications, and unpublished checklists. To estimate ranges for each species we applied a mixture of a niche-based approach (by underlying records with habitat maps such as altitudinal relief, vegetation zones, precipitation or minimum winter temperature) and a consideration of historical and species-specific constraints. The limits of many species within Malesia, for example, are determined to a large extent by historical dispersal limits rather than by habitat alone, so in that region we did not extend species ranges beyond actual records. Uneven sampling efforts in different regions (see also Fagan and Kareiva, 1997; Soberón *et al.*, 2000; Graham *et al.*, 2004) or the likelihood of finding, correctly identifying or reporting different species was carefully assessed on a species-by-species basis in order to interpret data. Considering all these factors, the best possible estimate of each species range was digitized. We did not use an explicit computer model to estimate ranges as 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. Cowley *et al.*, 2000; Zaniewski *et al.*, 2002). All range maps and island checklists, as well as an example of the process of range estimation, are given in Beck and Kitching (2004), and more details and discussion of the procedure can be found in Beck (2005). Area sizes of these estimates are used here as a measure of range size. Other measures, such as minimum convex polygons around records, correlate well with these estimates (Beck *et al.*, in press a). To explore effects caused by the spatial extent of range measurement (i.e. comprehensive vs. partial range), we took those parts of the global range estimates that fall into Southeast Asia and Malesia and used them as partial, subcontinent-wide range estimates. Such regional restrictions are commonly found in macroecological studies and may change the apparent range–size relationships in an assemblage (Beck *et al.*, in press a).

Quantitative light trapping data of sphingid moths were compiled from publications, unpublished collections, and our own fieldwork across Southeast Asia (see Online Appendix). Only sites with more than 12 recorded species (≈ 50 specimens) were used for analyses. Our data showed that on average more than 75% of the locally present species richness was recorded during short-term (≈ 6 nights) light trapping sessions. Furthermore, mark–release–recapture experiments indicated that the attraction of nocturnal sphingids to light does not differ between species (Beck and Linsenmair, in press). Thus, light trapping data are good indicators of the relative abundance (or frequency) of nocturnal species at a site.

The regional 'commonness' of species (on a 4-, in one case 5-, point ordinal scale) was estimated by long-term collectors (see Fig. 1 and Online Appendix). These data result from many years' experience with the local frequency of species, thus filtering out atypical population densities. Furthermore, 'commonness' data contain some extremely rare species that were not recorded in the quantitative sampling.

Methods of analysis

Quantitative abundance data were normalized by log-transformation (see Discussion). Range area data show a considerable 'normalization' after log-transformation, but still contain a left-skew (Beck *et al.*, in press a). However, within single sampling sites they do not deviate significantly from normality (KS tests, $P > 0.05$).

Product–moment correlations were calculated between range areas and local abundances for each site. Fisher's z_r was then used as an effect size measure for meta-analysis (Rosenberg *et al.*, 2000). A fixed-effects model allowed us to assess the average effect size and its confidence intervals. Continuous and categorical models were used to explore effects of various sample site parameters on effect sizes.

Spearman rank correlations were used to test the relationship between range areas and commonness assessments. Rank correlations of data for diurnal taxa were calculated separately (where available), as they are based on other sampling methods.

Correlations of species' characters may give misleading results due to the statistical non-independence of data from species that share a common phylogeny (Freckleton *et al.*, 2002). We have previously shown a weak, but significant, phylogenetic autocorrelation in range size data (Beck *et al.*, in press a), whereas this is questionable for means of local frequencies [depending on whether raw or transformed data are considered (Beck, 2005)]. Independent contrasts were calculated (Felsenstein, 2004) in an attempt to free data from autocorrelation (Garland *et al.*, 1999), using the taxonomic classification in Kitching and Cadiou (2000) and some

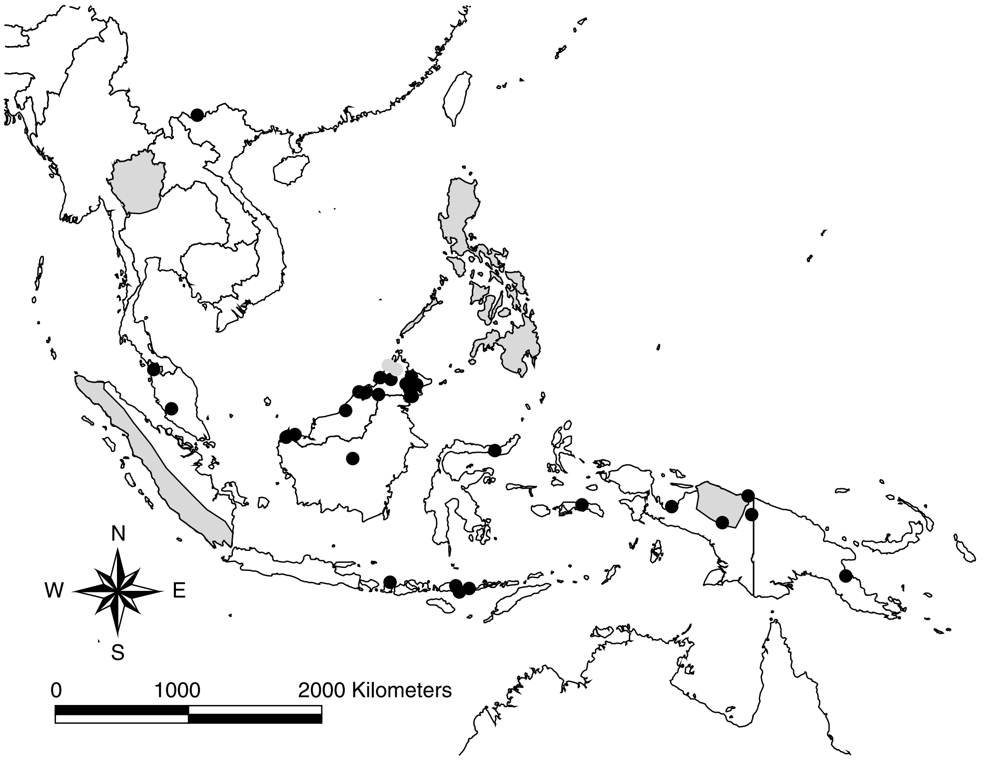

Fig. 1. Locations of 58 quantitative sampling sites with ≥13 species (mostly equivalent to ≥50 specimens) as well as the approximate extent of sampling regions (shaded) from which ordinal abundance estimates were available. Ordinal data from Peninsular Malaysia stem from a single sampling site in the Genting Highlands. Note that some sites are so close to each other that they appear as one point on the map. See Online Appendix for details and data sources.

unpublished updates as a substitute for a phylogeny. Branch lengths were set to 1 except at unresolved nodes, where they were set to 0.0001 (Felsenstein, 2004). All analyses were performed on species-level data as well as independent contrasts.

RESULTS

Range sizes were available for 380 sphingid species found in Southeast Asia (Beck and Kitching, 2004) (three further species were only recently described and are not included in our data), and more than 16,000 specimens provided quantitative abundance data for 144 species at 58 sites. 'Commonness' data from five different regions (see Fig. 1) could be retrieved for 284 species.

Quantitative data

Eight of 58 local RARs (Fig. 2) are significantly positive ($P < 0.05$) for species-level data, and nine for independent contrasts. A summary of effect sizes (z_r) shows a significantly positive effect [species-level data: $z_r = 0.18$ (99% $\mathrm{CI}_{\mathrm{bootstrap}}$: 0.09–0.27); contrasts: $z_r = 0.16$

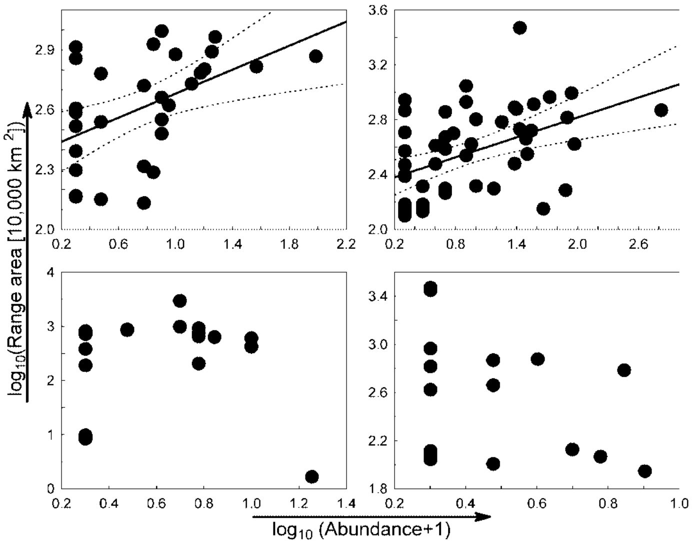

Fig. 2. Examples of RAR plots. The top two graphs show significantly positive relationships (both from Borneo: site B3, $n = 30$, $r = 0.48$, $P < 0.01$; site B8, $n = 50$, $r = 0.46$, $P < 0.001$). The bottom two graphs show non-significantly positive (left, from Flores: site BAJ2, $n = 20$, $r = 0.01$, $P = 0.98$) and negative (right, from New Guinea: site IJ3, $n = 16$, $r = -0.34$, $P = 0.19$) relationships.

(0.04–0.25)]. Effect sizes were analysed for their total heterogeneity, Q_T, testing the null hypothesis that variability of effect sizes is solely due to sampling error (Rosenberg *et al.*, 2000). For species-level data, effect sizes do not indicate higher than random heterogeneity ($Q_{T(df=57)} = 68.4$, $P = 0.14$). However, heterogeneity becomes highly significant for independent contrast data ($Q_{T(df=57)} = 85.2$, $P < 0.01$). Therefore, we explored effect size data for differences between groups of sample sites such as region, habitat disturbance, and elevation.

Figure 3 shows effect sizes separately for regions. Differences are not significant (see confidence intervals), but strongly suggest a geographical gradient from west to east in the archipelago: west of Sulawesi all regional effect sizes are greater than zero, whereas no significant positive effects could be found in the east. Patterns are almost identical for independent contrast data (not shown).

Similarly, only in primary forests could a clearly positive effect be found, whereas secondary forests and open, heavily disturbed sites have effect sizes that are not significantly greater than zero (Fig. 4). A continuous meta-analytic model by site elevation shows a very weak negative regression of effect sizes with altitude that is non-significant for species-level data ($P_{\text{rand}} > 0.20$) and becomes a weak trend ($P_{\text{rand}} < 0.10$) if contrasts are considered.

In addition, no qualitative distinction of results based on species-level data and independent contrasts was observed. Partial range sizes yield ten positive range–abundance correlations; the average effect size from meta-analysis [$z_r = 0.227$ (95% $\text{CI}_{\text{bootstrap}}$: 0.150–0.294)] is non-significantly larger than those for comprehensive ranges.

We also calculated mean frequencies of species across the sampling sites where they occur and tested for a relation to range sizes. Product–moment correlations (Table 1) generally

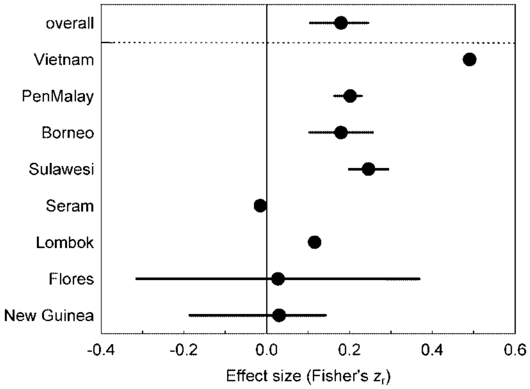

Fig. 3. Average effect sizes and 95% confidence intervals (bootstrap) as a result of categorical meta-analysis for RARs at 58 sites from different regions (islands). The numbers of sites in each region are: Vietnam ($n = 1$), Peninsular Malaysia ($n = 2$), Borneo ($n = 43$), Sulawesi ($n = 2$), Seram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

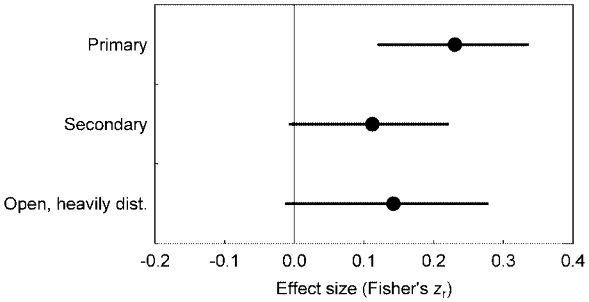

Fig. 4. Average effect sizes and 95% confidence intervals (bootstrap) as a result of a categorical meta-analysis for RARs from sites with different degrees of (mostly anthropogenic) disturbance. The numbers of sites in each disturbance class are: primary forest ($n = 26$), secondary forest ($n = 20$), heavily disturbed, open sites ($n = 10$). The graph shows results based on species-level data; the patterns based on independent contrasts are very similar (not shown).

Table 1. Product–moment correlations of mean frequency (arcsin-square root transformed) and range area for Southeast Asian sphingids

	n	r^2	P
Range–mean frequency	132	0.006	0.385
Contrasts	131	0.029	0.051
Partial range–mean frequency	132	0.006	0.381
Contrasts	131	0.001	0.797

Note: All relationships are (non-significantly) negative.

yielded non-significant results, whereas null model simulations (Table 2) supported expected data boundaries of a positive, polygonal relationship (Gaston, 1996).

Ordinal data

In four out of five regions we found a positive rank correlation between estimated local commonness and comprehensive range size (Fig. 5, Table 3). Furthermore, three of the four significant correlations persist after controlling for effects of phylogeny. Range–abundance correlations appear weaker in day-active taxa and are non-significant in three of four regions (Table 3). However, all relationships are positive with $R > 0.25$. Therefore, non-significance might be at least partly a consequence of low sample sizes (number of species).

Table 2. Results from *range area–mean frequency* null-model simulations (10,000 randomizations, asymmetric boundaries; *EcoSim*) (Gotelli and Entsminger, 2004) for comprehensive and partial (Southeast Asia wide) range estimates

	Comprehensive range		Partial range	
$P_{(\text{obs} \neq \text{sim})}$	Species-level	Contrasts	Species-level	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

Note: Transformed data were used to allow for a direct comparison to regression results (Table 1). Raw data (not shown) did not yield qualitatively different results.

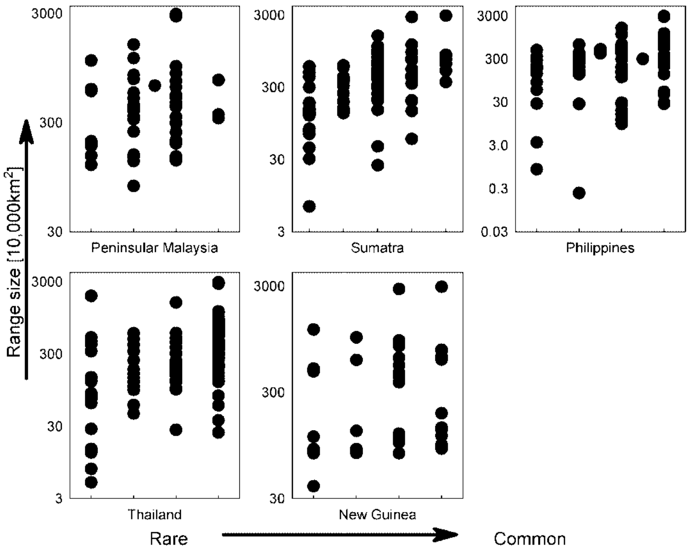

Fig. 5. Relationships between comprehensive range and ordinal commonness estimates in five regions for night-active, light-attracted sphingid species. Data for day-flying species are not shown. See Table 3 for statistical tests.

Table 3. Rank correlations of comprehensive range and 'commonness' in night-active and day-active sphingid species

		Species-level data		Contrasts	
	Species (*n*)	*R*	*P*	*R*	*P*
Night-active					
Thailand	127	0.53	<0.001	0.37	<0.001
Peninsular Malaysia	59	0.13	0.35	−0.08	0.53
Sumatra	91	0.57	<0.001	0.45	<0.001
Philippines	89	0.33	<0.01	0.32	<0.01
New Guinea	46	0.46	<0.01	0.22	0.19
No. of significant correlations			*4*		*3*
Day-active					
Thailand	30	0.27	0.15		
Peninsular Malaysia	13	0.38	0.21		
Sumatra	23	0.32	0.14		
Philippines	32	0.48	<0.01		
No. of significant correlations			*1*		

Note: Independent contrasts were not calculated for day-active taxa as their phylogeny is insufficiently resolved. No data for day-active genera were available from New Guinea.

DISCUSSION

This study provides empirical support of a positive RAR in tropical insects on a spatially extensive scale. Previous studies on tropical insects [e.g. dung beetles in Borneo (Hanski, 1982) and West-Africa (Hanski and Cambefort, 1991) (see also Pantoja *et al.*, 1995; Krüger and McGavin, 2000)] covered considerably smaller regions and used partial ranges as a measure of geographic distribution. A number of studies on tropical butterflies, however, showed that in a conservation-related context, local rarity of species is usually associated with small geographical ranges (Thomas, 1991; Spitzer *et al.*, 1993; Hill *et al.*, 1995; Hamer *et al.*, 1997; Ghazoul, 2002).

Effects of measurements and phylogeny

For sphingids, positive RARs were found for 'commonness' assessments in several regions as well as for the summed effect of single-site correlations of quantitative data (in meta-analysis), but not for 'conventional' measures such as (transformed) mean abundance (although null-models analysis confirmed expected trends).

This indicates a methodologically important difference in local abundance measurements and their normalized means over a large spatial extent. Habitat heterogeneity, which leads to spatial variation in the local abundance of a species, results in an irregular abundance distribution for which means, as well as maxima or single local figures, cannot be a sensible measure (Brewer and Gaston, 2003; for similar conclusions, see Thompson *et al.*, 1998; Holt *et al.*, 2004). We suggest using meta-analysis as a suitable way to approach this problem, as it allows one to regress range area with local abundance in each habitat, yet still yields a summarizing, spatially extensive test result.

Analyses based on partial or comprehensive ranges did not differ much in overall results. However, partial ranges tended to produce stronger positive correlations (cf. Gaston, 1996). Our results provide some justification for using partial range measures as a proxy for unavailable comprehensive range data, albeit still on a subcontinent-wide scale [e.g. Europe-wide ranges in Quinn *et al.* (1997)].

Correcting data for phylogenetic non-independence is a standard procedure in macroecology (e.g. Blackburn and Gaston, 1998; Brown, 1999). However, there is a lot of disagreement as to whether it is always necessary or successful to apply the independent contrast method (e.g. Brown, 1999; Freckleton *et al.*, 2002). Previous analyses (Beck *et al.*, in press a) tentatively indicated that random walk models (as used for independent contrasts) might not be suitable to describe range size evolution. Furthermore, the 'phylogeny'-substitute that was used here contains no branch length information, has many unresolved nodes, and must generally be considered as approximate at best. We presented analyses for species-level data as well as independent contrasts (Blackburn and Gaston, 1998). A comparison of results shows that findings do not depend on whether species-level data or contrasts were used; contrast data mostly had weaker *P*-values and weaker correlation effects [as in many comparative studies (e.g. Garland *et al.*, 1999)].

Quantitative data in this study were log-transformed to meet assumptions of the parametric correlation statistics used in meta-analysis. However, transformations change the original data structure and may lead to artefacts in the results regarding the relationship investigated initially. We explored our results' sensitivity to data transformation by applying non-parametric, as well as parametric, statistics to raw (non-transformed) data with its often highly skewed distributions. Results for individual sites (see Online Appendix) differ in some cases, as they do for species-level versus contrast data, but overall the results are stable: meta-analysis of product–moment correlations of raw data indicate a significant effect [$z_r = 0.078$ (95% $\mathrm{CI}_{\mathrm{bootstrap}}$: 0.024–0.127)], and the data clearly show the same geographic trend as presented for log-transformed data (not shown). Furthermore, non-parametric correlations (for which the meta-analytic approach is not feasible) confirm the reported patterns: of 58 local RARs, 11 are significant at $P < 0.05$, all of which are positive (Spearman's $R > 0.3$) and all but one (KEL1, Flores) are in the western part of the archipelago.

Effects of region and habitat type

Categorical meta-analyses were used to investigate differences of range–abundance correlations along some *a priori* chosen sample site parameters (region, habitat disturbance). Significantly positive 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. Various features of sphingid communities (e.g. regional species richness, proportion of subfamilies) are known to change along a northwest–southeast gradient through the Malesian archipelago (Beck *et al.*, 2006). For many Southeast Asian species, New Guinea and the Bismarck Archipelago are an eastern distribution limit, as only few wet-tropical habitats can be found further south and east. Furthermore, we suggest that after speciation in the eastern part of the archipelago, new taxa have to cross significant dispersal barriers to attain large range sizes (Beck *et al.*, 2006). This process might distort the 'normal' pattern of the RAR. Alternatively, it could be argued that the regional gradient is an artefact of lower sample sizes in the east: eastern islands are poorer in species (Beck *et al.*, 2006), and fewer specimens were caught there than in the west. Both factors contribute to lower sample sizes (number of species) in correlations. Although z_r is indeed positively correlated with sample size for species-level data (log(N), 58 sites: $r^2 = 0.069$, $P = 0.047$), this relation is lost in effect sizes of independent contrasts ($r^2 = 0.044$, $P = 0.110$). It thus cannot be responsible for the same geographic trend in contrast-based analyses (not shown). The proportion of subfamilies changes with longitude (Smerinthinae decline towards the east), and subfamilies differ in dispersal ability and life history (Beck *et al.*, 2006), both of which might be suspected to influence range–abundance relations. However, we did not find different effect sizes in range–abundance correlations between the three sphingid subfamilies (data not shown). At present, we cannot offer a convincing causal explanation of the reported regional pattern, and it remains to be seen if it is a peculiarity of sphingid assemblages or if it can be found in other Southeast Asian taxa as well.

Causal explanations of the range–abundance relationship

Gaston *et al.* (1997) reviewed and evaluated a number of hypothetical mechanisms for a positive RAR. Of those, the niche-breadth hypothesis can be addressed by existing data on sphingids: species with wider ecological niches might be more successful in utilizing local resources, thereby acquiring high local abundance, and they might disperse more easily as they can find at least some useful resources in a new site. The dietary breadth of herbivorous insects is certainly an evolutionarily important niche dimension (e.g. Mitter *et al.*, 1991) and has been used previously to test niche breadth effects on RARs (Quinn *et al.*, 1997). Only one of the three predictions of the hypothesis (Gaston *et al.*, 1997) could be addressed quantitatively: Range size correlates with species' larval diet breadth (on plant family level, data from Robinson *et al.*, 2001 and unpublished updates) (Fig. 6). Hence, widespread taxa indeed use more host plant families, although undersampling might bias host plant records to an unknown degree and in an unknown direction (Fiedler, 1998). A correlation with mean abundance, however, is much

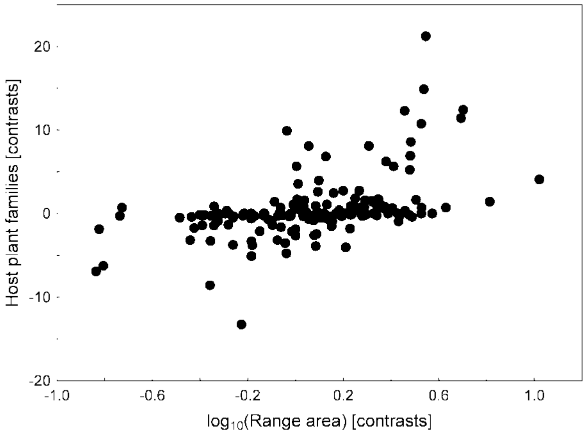

Fig. 6. Range area and dietary niche (number of recorded host plant families) of Southeast Asian sphingid caterpillars (independent contrast data). Spearman rank correlations are significant for species-level data (not shown: $n = 166$, $R = 0.54$, $P < 0.001$) and independent contrasts ($n = 165$, $R = 0.53$, $P < 0.001$).

weaker ($n = 91$, $R = 0.22$, $P < 0.05$) and non-significant if independent contrasts are considered ($n = 90$, $R = 0.05$, $P = 0.68$; dietary breadths are phylogenetically autocorrelated), and no positive relationship between local abundance and diet breadth was found in a meta-analysis of site-by-site comparisons (Beck, *et al.*, in press b).

The niche-breadth hypothesis furthermore suggests that the measurement of species abundance in 'uncommon' habitats leads to negative RARs as such habitats favour specialists (Gaston, 1996). We failed to find sufficient specimens for analysis in *a priori* chosen rare forest types on Borneo, such as mangroves or heath forests, whereas a forest on ultra-basic soil did not contain an unusual sphingid assemblage (SIL1, see Online Appendix). However, it might be assumed in this context that disturbed sites were relatively rare habitats in the less populated parts of Southeast Asia until the onset of industrialized logging about 50–70 years ago (e.g. Marsh and Greer, 1992). The reduced strength of range–abundance correlations in disturbed habitats might be interpreted as support for the hypothesis 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). It is difficult to assess how realistic this scenario is – for very slow dispersers such as termites, Pleistocene habitat differences are still evident in modern primary forest communities (Gathorne-Hardy *et al.*, 2002), whereas many sphingids appear to be very good dispersers (Beck *et al.*, 2006). 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 anecdotally: *Daphnis nerii*, *Macroglossum pyrrhosticta*, and possibly *Hippotion rosetta* have successfully colonized Hawaii during the last 30 years, most likely by human traffic. If sorted by declining rank, they are placed 7, 17, and 20 respectively of 380 for range areas, whereas ordinal commonness assessments (in Southeast Asia) mostly place them in the upper mid-field in those regions where they occur.

In addition to the mechanisms reviewed by Gaston *et al.* (1997), two 'unified theories' predict and explain a positive RAR from general model assumptions. Whereas Hubbell's (2001) complex neutral theory is not testable with the existing data, McGill and Collins' (2003) idea is relatively straightforward. Based on several assumptions about a regular spatial distribution of abundance and an overlap of species ranges with different centres, they were able to model a positive range–abundance distribution. If the model were a sufficient explanation for RARs, then species with identical distribution centres should not exhibit a RAR. This cannot, of course, be tested precisely with the present data, but it can be attempted with several approximations. Distribution centres of species were calculated as the mean of their latitudinal and longitudinal extremes. We then used only those species that have their distribution centre within a 1000 km radius around north-central Borneo for tests of RARs at 42 local sites on Borneo (including a total of 34 species). The summarized effect size from meta-analysis is $z_r = 0.278$ (95% $\mathrm{CI}_{\mathbf{bootstrap}}$: 0.132–0.401). Contrary to the prediction, it is not smaller but (non-significantly) larger than for all species, and thus the hypothesis is rejected.

APPENDIX

Locations, sample sizes, range–abundance correlations, and data sources for all sample sites and regions. Available as an electronic supplement at: http://www.evolutionary-ecology.com/data/2003appendix.pdf

ACKNOWLEDGEMENTS

We are very grateful to the many people who let us use their unpublished data, in particular Dr. Jeremy D. Holloway and Henk van Mastrigt [see acknowledgements in Beck and Kitching (2004) for a full listing]. We thank various persons and institutions for permission and logistic support of fieldwork in Southeast Asia, including Dr. Chey Vun Khen (FRC), Dr. Jamili Nais (Sabah Parks), the DVMC, Moses Jalawatu, Henry Barlow, and Wilem Kayoi (Dinas Kehutanan Jayapura). The EPU of Malaysia issued a research permit for J.B. The project was supported financially by scholarships from the 'Graduiertenkolleg' (German Research Council, DFG), the DAAD, and the Sys-Resource programme of the EU.

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