THE LATITUDINAL DISTRIBUTION OF SPHINGID SPECIES RICHNESS IN CONTINENTAL SOUTHEAST ASIA: WHAT CAUSES THE BIODIVERSITY 'HOT SPOT' IN NORTHERN THAILAND?

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ABSTRACT. **–** The species richness of most organisms follows a latitudinal gradient with higher richness towards the equator. However, recently available data on sphingid moths from continental Southeast Asia indicate an almost inverse pattern, with a peak of species richness in Thailand's Chiang Mai province (and surrounding areas) and a decline towards the north as well as to the south. We analyze original distribution records and quantitative local samples to explore ecological effects and the impact of sampling biases on this pattern. Our analyses indicate that the pattern is unlikely to be an artefact of the large differences in sampling effort in different regions. In a comparison of the four best-sampled regions on a north-south gradient, we did not find significant differences in endemism. The species richness of northern Vietnam might benefit from an overlap of subtropical and tropical faunas, but data do not suggest such an effect in more southerly regions. A 'peninsula effect', possibly mediated by area sizes, appears a likely explanation of the observed pattern. The altitudinal relief of regions might also contribute to species richness patterns, as local diversity apparently increases with altitude, and montane regions have more endemics. We conclude that, despite strong congruencies in (estimated) species richness and sampling effort, ecological effects have the potential to create the unusual latitudinal pattern. We discuss methodological consequences of this finding.

KEY WORDS. **–** Hawkmoths, Lepidoptera, peninsula effect, range size, sampling bias, Sphingidae.

INTRODUCTION

On continental and global scales, the species richness of most organisms follows a latitudinal gradient with higher richness towards the equator (Rosenzweig, 1995). Much effort has been undertaken to investigate and explain this gradient (Chown & Gaston, 2000), and the focus in research has now moved from descriptive documentation to testing of proposed causal factors (e.g. Hawkins & Porter, 2001; Sax, 2001; Koleff & Gaston, 2001; Hawkins & Diniz-Filho, 2004; Hawkins et al., 2006).

Beck & Kitching (2004) compiled original distribution records for hawkmoths (Lepidoptera: Sphingidae) from Southeast Asia and Malesia and used them to estimate overall geographic ranges for those species in the region. These maps were used to estimate and analyse patterns of regional species richness in the tropical, insular parts of the region (Beck et al., 2006a), where regional species richness is high in the west but low in the east.

The estimated species richness of sphingid moths in continental Southeast Asia [see Fig. 1A for sketch, Beck & Kitching (2004) for a more detailed map] indicates a notable exception from the typical latitudinal pattern. Species richness peaks in the north, particularly in northwestern Thailand (i.e., Chiang Mai province), whereas it is considerably lower in the Malay Peninsula. However, sampling intensity also peaks in northwestern Thailand (Fig. 1B). Although using range estimates decreases bias in the data caused by undersampling

to a certain degree, heavily neglected regions may still not provide reliable diversity assessments. We consider that Burma, particularly its western part, together with southern Laos and Vietnam, and most of Cambodia, are so poorly sampled (due to historical and recent logistic conditions) that richness estimates in these areas almost certainly under-represent real values to an unknown extent. We will therefore not discuss the low apparent species richness in these areas any further. However, Thailand, the Malay Peninsula, and northern Vietnam are relatively well-sampled (Fig. 1B) and range estimates in northern Burma are often supplemented by records from well-sampled neighbouring regions in India and Bangladesh.

In this paper we discuss possible ecological causes of the latitudinal pattern of species richness in Southeast Asia against the alternative explanation of a sampling artefact. By analyzing distribution data and quantitative local samples, we will confirm the existence of the mapped pattern and evaluate various hypotheses as to its ecological causes: (1) An overlap of temperate and tropical faunas (possibly mediated by elevational stratification), (2) the existence of special habitat conditions, or (3) a 'peninsular effect' (Brown & Opler, 1990) could allow the occurrence of more species in the northern than in the southern part of Southeast Asia.

MATERIAL AND METHODS

Details on the compilation of >35,000 original distribution records of Southeast Asian species and their use to estimate the geographic range for each species can be found in Beck & Kitching (2004; note that one 'record' refers to a particular combination of species, location, sampling year and source, and may therefore refer to one up to hundreds of specimens). Overlaying these range maps led to the species richness estimates discussed here.

We use data on the elevation of sampling sites where supplied (in northwestern Thailand this is available for 70% of records) to investigate altitudinal stratification. We categorized records as 'lowland' (≤600 m), 'intermediate' (601–1699 m) or 'montane' (≥1700 m), and classified species as elevation-specific if they were only recorded in one of these zones (the number of records per elevation-specific species varied between one and 158, median = 8).

We used the northernmost and southernmost recorded latitudes of species to analyse range extent and position for the faunas of northern Vietnam (north of 20°N), northwestern Thailand (north of 18°N), central Thailand (13–17°N) and the Malay Peninsula (called 'Malaysia' hereafter for brevity,
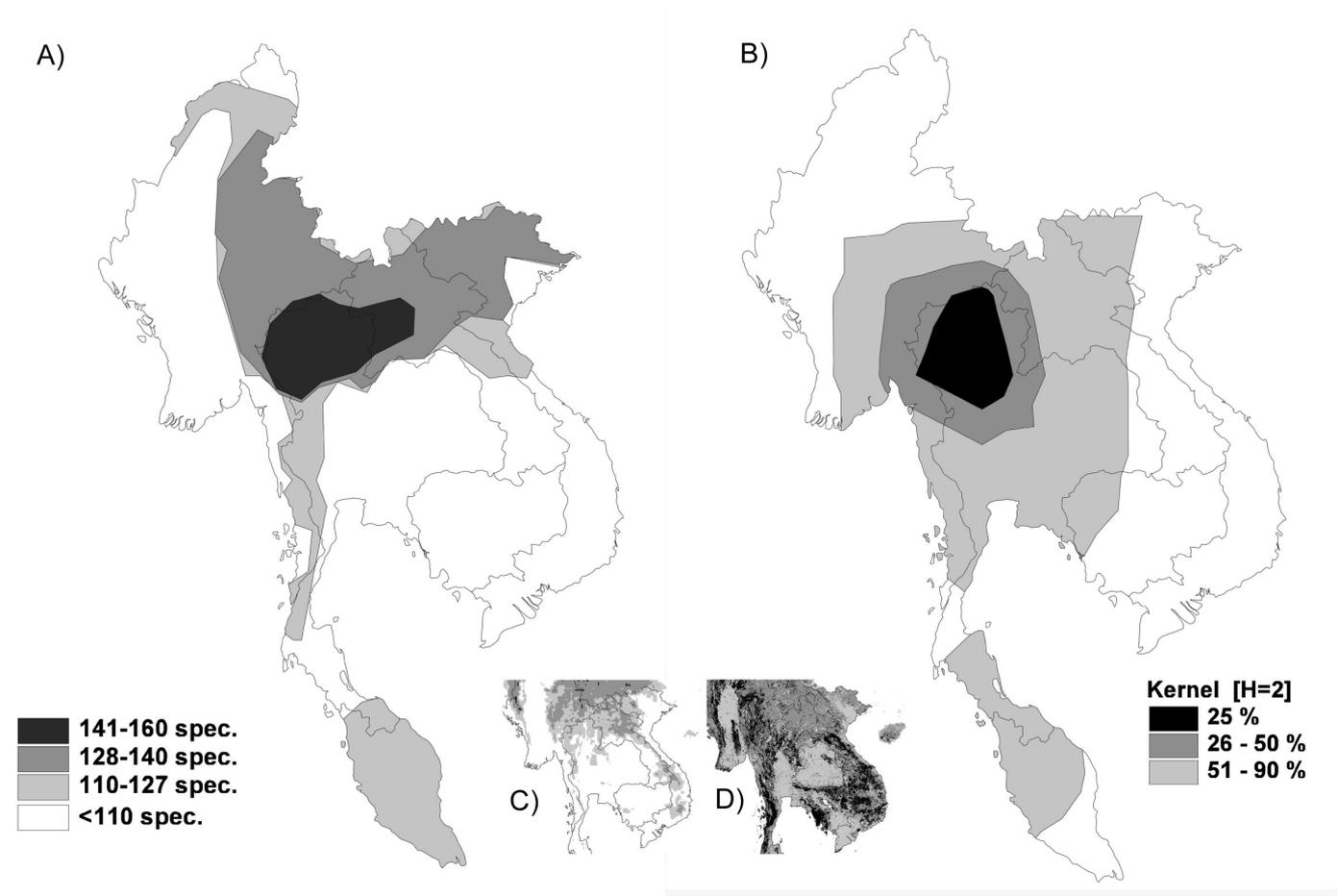

Fig. 1. A, Estimated species richness (simplified from Beck & Kitching, 2004); B, Sampling intensity (kernels of original distribution records, smoothed; software by Hooge et al., 1999); C, altitudinal zonation (from digital elevation model, http://www.ngdc.noaa.gov/mgg/global/seltopo.html). Elevation classes are [m]: 0–500 (white), 501–1000, 1001–1500, 1501–2000, >2001 (black); D, Landscape types (simplified from remote sensing data, http://www-gvm.jrc.it/glc2000). Agricultural and highly disturbed areas are printed in light grey, mosaic and bush in dark grey and closed forests in black.

Table 1. Approximate latitudinal position, number of 1° grid cells, and recorded and F3-estimated species richness for four regions of continental Southeast Asia.

Region	Latitude [°N]	Grid cells	Rec.	F3
Northern Vietnam	20.0 – 23.5	13	123	162
Northwest Thailand	18.0 – 20.5	10	157	188
Central Thailand	13.0 – 17.0	22	135	159
Malaysia	1.5 – 6.5	12	109	154

though including data from Singapore and excluding data from Borneo).

As an alternative estimate of regional species richness (independent of the GIS-based estimates of Beck & Kitching, 2004), we applied the regional estimator "F3" (Rosenzweig et al., 2003; software WS2M, http://eebweb.arizona.edu/diversity) to distribution data in 1-degree grid cells. This estimator has been shown to provide relatively good estimates for Southeast Asian hawkmoth data (Beck & Kitching, in press).

We used local, quantitative light trapping samples from Vietnam, Thailand and Malaysia (see Acknowledgements) to assess true local species richness by applying the abundance-based coverage estimator (ACE; Colwell et al., 2005). Moths were hand-sampled from a white sheet that was illuminated by light sources rich in UV wavelengths (backlight or Mercury-Vapour, depending on location). We also calculated the Fisher's α diversity index for easy comparison with published data from other regions (e.g. Borneo, Beck et al., 2006b). For this, we used only local samples of >25 individuals.

RESULTS

Local and regional richness estimates

The analysis of species richness in grid cells from four regions (Table 1), shows that not only recorded but also F3-estimated species richness follows the GIS-estimated pattern indicated in fig. 1A. The unusual relation between latitude and species richness is therefore not the consequence of erroneous range estimates in Beck & Kitching (2004). F3 estimates are generally higher than range map-based figures from Beck & Kitching (2004), a property that was also found in comparisons in other regions (Beck & Kitching, in press).

Estimated local species richness from quantitative samples increases with increasing latitude (Fig. 2), similar to the pattern found for estimated regional species richness (Fig. 1A, Table 1). This strongly suggests that the latter pattern is not an artefact despite its close resemblance to regional sampling intensity (Fig. 1B). ACE-estimates correlate with the number of sampled individuals (N = 9, r^2 = 0.77, p <0.01), although a species richness estimator should ideally be independent from sampling intensity. Fisher's α scores (which are independent of sampling intensity) indicate that local and regional diversity patterns are even more congruent (see caption of fig. 2) than the ACE-estimate suggests. A further quantitative sample from Malaysia (Pasoh Forest Reserve)

has even lower scores of Fisher's α, but was excluded from the analysis because the species composition suggests that the sample comes from a dense forest undergrowth where only few sphingid species can be found (75% of individuals were *Daphnusa ocellaris*; cf. Schulze & Fiedler, 1997). At another site in Malaysia (Genting highlands; H. Barlow, pers. comm.), 72 species were recorded, but these data were collected over more than 20 years and temporal species turnover (Beck et al., 2006b) has probably inflated this list above the species richness present at any one time.

We tested median Fisher's α values for significant differences, using the samples from northern Southeast Asia (Thailand & Vietnam) and Malaysia, and those from 57
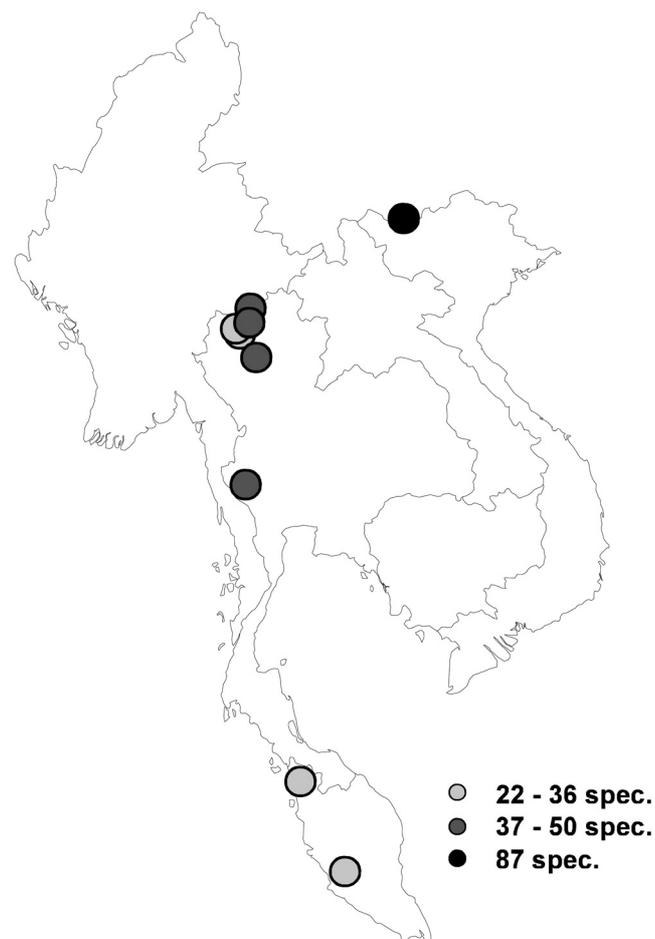

Fig. 2. Estimated local species richness (ACE) from nine quantitative light trapping sites. Fisher's α, an alternative measure of local diversity (not shown), is lowest at the Malaysian sites (α = 7–13) and highest at a montane site in Northwestern Thailand (α = 30), whereas the Vietnam sample and other Thai sites score intermediately (α = 11–21).

Legend:
22 - 36 spec.
37 - 50 spec.
87 spec.

quantitative sites on Borneo (Beck et al., 2006b), which is similar biogeographically and in regional species richness to the Malay Peninsula (Beck et al., 2006a). Sites in northern Southeast Asia have significantly higher α-values than sites on Borneo (Kruskal-Wallis ANOVA, N = 66, $H_{df=2}$ = 16.5, p <0.001; multiple z-test: z = 4.0, p <0.0001), whereas differences between the continental regions are not significant (z < 1.1, p >0.85).

Geographical distribution of species and species richness patterns

Species in Malaysia typically have the centre of their latitudinal range several degrees north of the region (see Fig. 3; possibly less land area in the insular south hinders range expansion of species), whereas in Thailand the majority of species are centred slightly (Central Thailand) or considerably (Northwestern Thailand) south of these regions. Only in Northern Vietnam does a fraction of subtropical species have their median distribution centre roughly in the latitudes of the region, whereas the tropical part of the fauna is centred some 10 degrees further south. Only here do we observe a bimodal distribution (Fig. 3), indicative of faunal overlap.

There is no difference in the median latitudinal extent of species (cf. Rapoport's effect, Gaston et al., 1998) between the four regions (KW-ANOVA: $H_{df=3}$ = 2.6, p = 0.46).

We classified species as geographically restricted if their recorded latitudinal range was five degrees or less. The fauna of Malaysia contains only one such restricted species, whereas Central Thailand has four, Northwestern Thailand has 10, and Northern Vietnam has 6. These proportions of latitudinally restricted species do not differ significantly from chance expectations based on the species richness of each region (2 x 4 table, χ^2 = 5.4, p = 0.14). Furthermore, excluding restricted species does not change to overall distribution of recorded species richness (Table 1). Thus, local endemics are not an explanation for observed species richness patterns.

We could classify 47 species from Northwestern Thailand (of 150 species with altitude information) as specific to one zone, whereas all others were classified as non-specific (27 of the non-specifics were recorded in all three altitude zones, the majority of others in both lowland and intermediate zones). Altitudinal niches of species are related both to latitudinal extent (KW-ANOVA, N =150, $H_{df=3}$ = 26.4, p
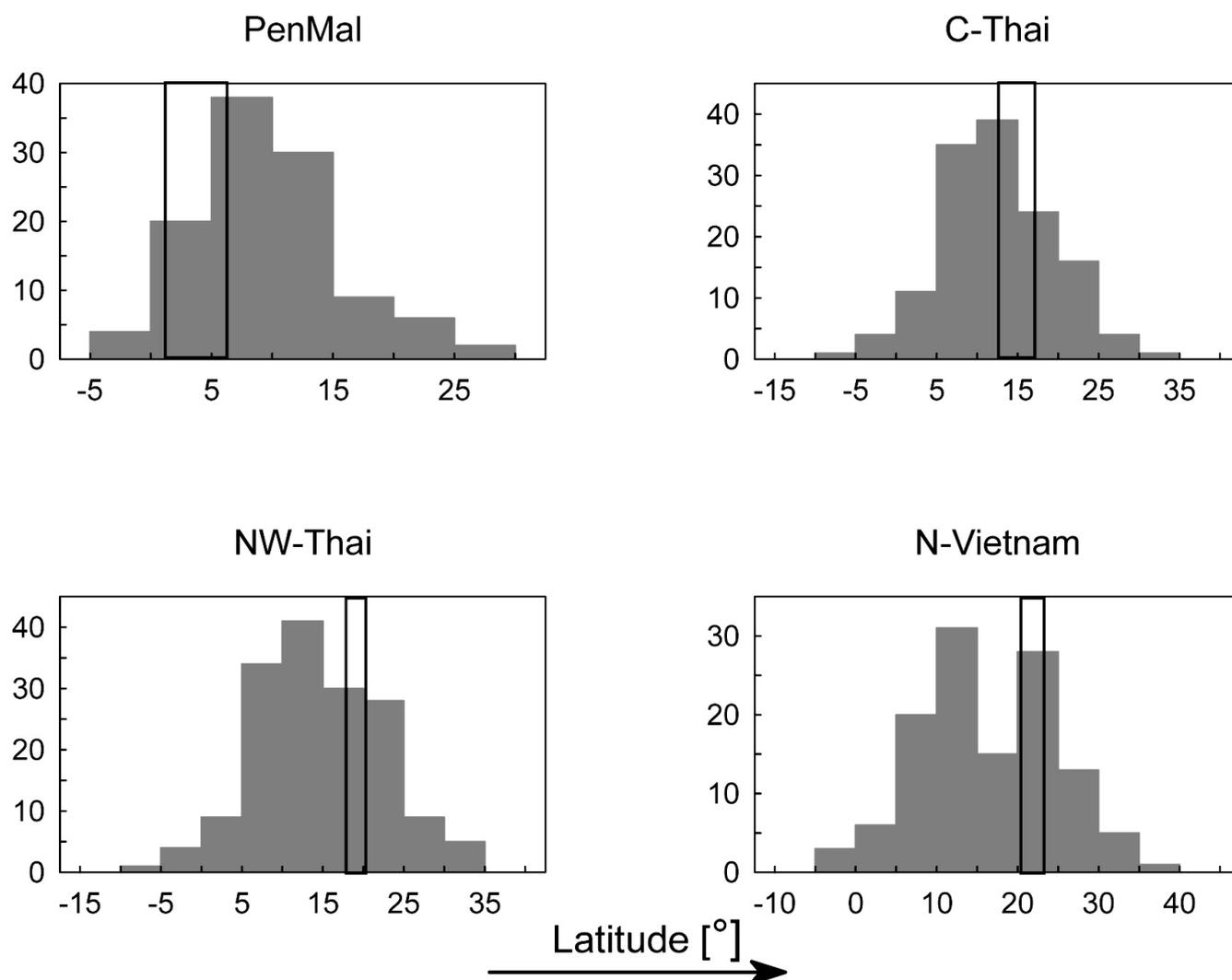

Fig. 3. Abundance (number of species, y-axis) and the latitudinal mean of their range in four regions. Black bars indicate the approximate latitudinal extend of the regions under investigation.

<0.0001) and latitudinal position (average of latitudinal extremes; $H_{df=3} = 12.0$, p <0.01). Montane species have a smaller median latitudinal extent than all other niche classes (i.e., there are more endemics in montane habitats; z > 3.1, p <0.02), and ranges of montane species are at significantly more northern latitudes than lowland or non-specific taxa (z >2.8, p <0.02). However, there are no further significant differences between groups of taxa; in particular, lowland species are not more "tropical" in their distributions than intermediate and non-specific taxa. Thus, the higher terrain of Northwestern Thailand, and northern Southeast Asia in general (Fig. 1C), has the potential to contain some endemic and northern species, but the overall low number of montane specialists (nine species) makes this unlikely as a sole explanation of the observed richness gradient. We could not apply such analyses to the considerably fewer data from the other regions.

Local habitat conditions

Northern Southeast Asia has, in comparison to Central Thailand, larger montane areas (Fig. 1C). In those local samples with altitude information, diversity (as Fisher's α) increases with altitude (N = 7, $r^2 = 0.72$, p <0.05; altitudes between ca. 480 and 1,800 m), whereas no relation with ACE-estimated species richness was found. Sphingid species richness peaks between 1,000 to 1,500 m in many mountainous landscapes of Southeast Asia and Malesia (J. Beck & I. J. Kitching, unpublished). The lack of highland areas in Central Thailand might therefore explain decreased species richness compared to areas further north, but it is not a strong explanation for low diversity in Malaysia, where mountainous landscapes are found.

Northwestern Thailand has a higher proportion of natural forest landscapes (Fig. 1D) and protected nature reserves (e.g., Gray et al. 1991; see http://www.trekthailand/net/list/ for latest data) than the rest of Thailand. However, we did not find a relation between habitat disturbance (in three classes) and local diversity for the eight sites with habitat descriptions available (data not shown). In Borneo, local sphingid diversity is not significantly influenced by human habitat disturbance (i.e., agricultural landscapes do not have a lower sphingid diversity than primary forests, Beck et al., 2006b), but species composition is. Thus, large, forested habitats might allow the persistence of forest specialists that are not found elsewhere, and hence increase regional species richness (we do not have detailed enough data to test this at continental sites). However, species richness decreases in Malaysia although large forests can be found there.

Area size and the geometric shape of Southeast Asia

Peninsulas have often, but not as a general rule, been noted for lowered species richness towards their tips (see Choi, 2004 for a recent study on Korean butterflies, references therein for more data). Various causal mechanisms have been proposed to account for this effect (Brown & Opler, 1990), among them island-biogeographic processes of colonization and extinction, in which equilibrium species richness depends on area and distance from the 'mainland', i.e. the base of the peninsula. We calculated the area of 3-degree latitudinal slices from the 'base' of the Southeast Asian peninsula (at 21°N) to its tip in Singapore. Area correlates positively with the species richness of slices (N = 7, $r^2 = 0.79$, p <0.01). Residuals of these correlations do not show any latitudinal pattern, but low values at latitudes of Central Thailand. Multiple regression approaches, including various combinations of maximum altitude of slices, distance from the base of Southeast Asia, and area did not yield significant results, nor did they lead to increased explanatory power of the model (data not shown).

Rising sea levels and associated changes in the shapes of coastlines since the Pleistocene have had considerable vicariance effects on sphingid assemblages across Malesia (Beck et al., 2006c). We used maps from Voris (2000; on-screen digitized in GIS software) to calculate areas of 3-degree slices for ancient shorelines 50 metres below those of today (analogous to the procedure above, from 21°N to the equator). A correlation with species richness of the slices, including species from Sumatra and Borneo (where applicable), is weak and non-significant ($r^2 = 0.23$, p = 0.27). However, a number of unknown variables, such as whether species went extinct or have shifted range since the Pleistocene, or how habitat changes during drier periods (Pickett et al., 2004) could have affected species distribution, make it impossible to interpret this finding unequivocally.

DISCUSSION

Our analyses have shown that the notion of a generally positive relationship between latitude and species richness on the Southeast Asian peninsula is not an artefact of Beck & Kitching's (2004) range estimation process, nor is it an artefact of the large differences in sampling effort in different regions (however, we think it is likely that the observed west-east pattern (Fig.1) across Southeast Asia is an artefact of under-recording in Vietnam and Burma).

In a comparison of the four best-sampled regions along a north-south transect, we did not find significant differences in endemism. The species richness of Northern Vietnam might be promoted by an overlap of subtropical and tropical faunas, but data do not suggest such an effect in Northwestern Thailand, the area with the highest species richness. Local habitat conditions, such as closed forest, do not lead to differences in local diversity, but might contribute to regional species richness by species turnover due to higher habitat heterogeneity (a hypothesis we could not test with our data).

An analogy between latitudinal and altitudinal peaks of species richness has been observed in various Southeast Asian Lepidoptera taxa. Within the family Geometridae, for example, the species richness of the subfamilies peaks (as far as known) at low altitudes and equatorial regions (Geometrinae), mid-elevations and northern Southeast Asia (Ennominae, Sterrhinae), or montane regions and higher latitudes (Larentiinae; J. D. Holloway, pers. comm.; see also

Sihvonen & Siljander, 2005). A pronounced mid-elevational peak in species richness of Sphingidae from many mountainous regions in Southeast Asia and Malesia (J. Beck & I. J. Kitching, unpublished data) fits well into this pattern, but a functional relation between latitudinal and altitudinal patterns (caused, e.g., by similar geometric constraints, or species' habitat choice) has yet to be investigated.

A 'peninsula effect', mediated by area sizes, appears as the most likely explanation of the observed pattern. Area has a very reliable relationship with total as well as local species richness in almost all investigated organisms across almost all spatial scales (e.g. Rosenzeig, 1995; Plotkin et al., 2000; Scheiner, 2003; Horner-Devine et al., 2004; see Beck et al., 2006a for sphingids in Malesia).

The altitudinal relief of regions might also contribute to species richness patterns, as local diversity increases with altitude in our data (up to 1,800 m), and montane regions (in Northwestern Thailand) have more endemics than other strata. However, in a multiple regression approach this factor did not significantly contribute to the explanation of patterns by area. Artefacts of low sampling intensity in southern Vietnam might have biased data in the analysis of these slices (e.g. underestimated species richness in montane regions between 9–15°N).

The decrease in species richness north of ca. 20°30'N (i.e., north of Thailand) probably represents the return of the 'normal' pattern of decreasing richness with increasing latitude outside of the peninsula region, but we cannot verify this without comprehensive data from more northerly latitudes. Unfortunately, our analysis of local samples does not lead to unequivocal results with regard to the Northern Vietnam sample (Fisher's α decrease with regional species richness, whereas ACE increases). Data indicate that ACE values are biased by sample sizes, but we still cannot exclude with certainty that an under-sampling bias is cause for the northern decline in species richness.

Our analyses have shown that despite strong resemblances of the geographic patterns of species richness and sampling effort (Fig. 1A, B), a number of ecological factors also have the potential to explain the unusual diversity gradient of Southeast Asian sphingid moths. At the same time, we provided evidence that observed patterns along the north-south gradient are unlikely to be a sampling artefact. A coincidence of species richness and sampling effort is possibly caused by the non-systematic way distribution data are sampled (Graham et al., 2004). The main objective of taxonomists and hobby-collectors, who do most field sampling, is maximizing species richness in samples, and particularly finding rare species, with a minimum of effort. They commonly exchange information as to where good sampling sites are located, both with regard to logistics (transport, sampling permits, etc.) and specimen numbers and species richness. This probably leads to a concentration of sampling effort in regions already known to be "good" (i.e. species-rich).

Geographic sampling biases must always be seriously considered in large-scale distributional records. However, as the effect outlined above is probably present in all distributional data sets, it is important to explore its general implication for statistical testing – if correlations of sampling intensity and species richness are not the result of an unidirectional cause-and-effect, but influence each other and interact (cf. Malakoff, 1999), their importance for the explanation of species richness (e.g., if tested against ecological parameters in multivariate statistical designs) might be overestimated.

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