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commentary

New insights on a classic topic: The biogeography of Southeast-Asian mammals

Investigating the fauna of Malesia, the insular region between Indochina and Australia, has a long history in biogeography. In relating the distribution of animals to geographic settings of the present and the past, A.R. Wallace (1869) has not only defined our discipline but also provided data and ideas that substantially aided understanding organic evolution (e.g., Davies 2008). Given the depth of investigation of the Malesian region by Wallace and subsequent researchers until today (see references in Woodruff and Turner 2009), it is surprising that the delineation of the region towards the north-west, i.e. between 'Sundaland' and the Indochinese continental region, and the causes for this faunal transition, remained out of focus for so long.

In their recent article, Woodruff and Turner (2009) have used data on mammal distributions to investigate the faunal transition between continental Southeast Asia and the Thai-Malay peninsula (Fig. 1), building upon earlier analyses of the group (e.g. Woodruff 2003, Hughes et al. 2003). Woodruff and Turner show that there is not, in contradiction to common presumption and earlier results (e.g., Cranbrook 1981, Hughes et al. 2003, de Bruyn et al. 2005), a well-defined Indochinese-Sundaic faunal boundary, but rather a ca. 800 km gap between a southern fauna of the Malay peninsula (south of 5ºN) and the continental fauna (north of 14ºN). In this region species richness is reduced, and even many widespread species have gaps in their distributions. The authors discuss sea level changes as an agent that may explain this pattern. In the following I will first appraise two methodological and conceptual features – namely, 'simplistically' relying on raw distributional data, and the consideration of ancient shorelines during times when sea levels were higher than today. I will then raise the issue of historical versus environmental explanations in biogeography, in relation to Woodruff and Turners' fine work.

Woodruff and Turner relied on actual presence records to analyze the limits of species' distribution. The nature of their study region, with a clear north-south orientation, allowed using latitudinal range limits as a simple measure of distribution. For all but the best-sampled regions and taxa of Europe and North America, such data are surely biased by undersampling – species may occur well outside recorded limits, but have not yet been found. A large number of methods, ranging from more or less clearly defined 'expert range assessments' to numerical models of species' ecological niches (e.g., Elith et al. 2006), have been proposed to correct for such biases. However, such estimates of 'true' ranges are unable, at present, to account for the effects of dispersal barriers or local extinctions (e.g., Munguía et al. 2008), but require a priori assumptions on distributional limits caused by historical factors. Any gain by correcting for undersampling would therefore be punished by an increased circularity of arguments when the aim is to define historically caused boundaries of distribution. Decisions on using range estimates or raw data must be weighted in light of the investigated system (i.e., degree of undersampling) and the questions asked, and in Woodruff and Turner's study this is clearly in favour of the 'oldfashioned' raw data approach taken by the authors. However, for good reasons the authors did not analyze east-west distribution patterns of species within Indochina, as massive undersampling in places like Burma, Laos or Vietnam would make most raw longitudinal data highly unreliable (but see Catullo et al. 2008 for an attempt to provide and use estimate data).

In their attempt to explain the latitudinal faunal patterns found, Woodruff and Turner turn to the fluctuations of sea levels (using latest geological data) and their implications on fusing and disrupting land areas over time. Many researches have tried to explain complex faunal patterns across the islands between Southeast Asia and Australia by changed shorelines during periods of lowered sea levels, when parts of the continental shelves fell dry and facilitated faunal exchange. However, the present study points out the potential importance of higher sea levels in causing local extinctions and distributions gaps that persist until today. These may have often been overlooked in earlier biogeographic studies in the region (cf. Woodruff 2003). Furthermore, they argue that the repetition and rapidity of change, rather than the creation of water straits as dispersal barriers, may have played a prominent role here. Their argument can be condensed to sea-level dependent contractions in available area sizes that led to regional extinctions within a once more widespread fauna. A concentration of faunal boundaries would then be expected where stable habitat, i.e. mountainous regions, is bordering the regularly flooded zones – and this is what has been found.

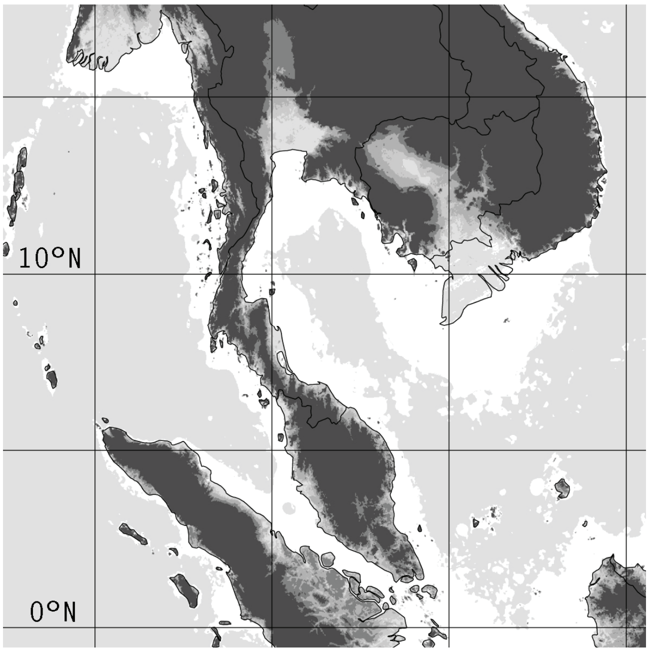

Figure 1. The Thai-Malay peninsula. Present-day coastlines, country borders, latitudes and longitudes (10 degree steps) are shown for orientation. To illustrate changes of the landscape with rising sea levels, the topographic profile of the land is shown on a six-point greyscale (0-5, 6-10, 11-25, 25-50, 51-100, >100 m). The effect of lowered sea levels can be assessed by the shallow-water region of the shelf (to -50 m depth), indicated by the white area in the sea. Data simplified from Amante & Eakins (2008).

Woodruff and Turner thoroughly discussed how additional processes could have affected species' geographic distributions in the region, and how future studies could support and test their proposed historical explanation. Of those, I want to focus here on the consideration of species' ecological niches, hence the importance of habitat conditions. How much of the observed pattern could actually be explained by present-day environmental differences between regions, rather than by historical idiosyncrasies? For example, Beck et al. (2007) observed a similar pattern of reduced species richness in the central peninsula in moths as Woodruff and Turner for mammals, but discussed present-day factors (lack of montane and near-natural habitats, present-day area), rather than historical accounts of sea level changes, as potential explanations. Irrespectively of the fact that Woodruff and Turner's study is based on much better data, and Beck et al. (2007) were simply unaware of the details of shoreline changes due to sea levels in the region, we should ask ourselves which kind of explanation should have precedence over the other in biogeography, and why.

Biogeography is currently divided in a historical branch and a (macro-)ecological branch, with the former investigating idiosyncratic events (in time and space) while the latter is dominated by the statistical search for stable patterns (of, e.g., environmental effects) as a consequence of, implicitly, equilibrium processes. It is far from trivial to judge what kind of explanation for observed patterns is more relevant. Recently, Ricklefs (2006; see also Ricklefs 2004) has argued convincingly that biodiversity is structured top-down from the regional (i.e., historical) to the local, whereas many ecologists implicitly seem to take the opposite approach. There is a growing trend to attempt fusing and weighting such historical and environmental explanations against each other (e.g., Graham et al. 2006; Hortal et al. 2008), of which biogeography will surely profit. Solving this problem is important, because biogeography is likely to transform from a 'ivory tower' academic discipline to one that is expected to predict, mitigate and reverse environmental problems related to 'global change'. Understanding the relative importance of environmental determinism and historical idiosyncrasy will be a key factor in achieving this: We can affect, in theory, the former by 'ecosystem management', while we can't turn back time on historical events.

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