Comment on "An Update of Wallace's Zoogeographic Regions of the World"

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Holt *et al.* (Report, 4 January 2013, p. 74) propose substantial modifications of Wallace's long-standing zoogeographic regions based on clustering of a pairwise similarity matrix of vertebrate assemblages. We worry about their compromised use of phylogenies and show that a fundamental point of their analysis—i.e., the delineation of new realms—is only weakly supported by their results and conceptually flawed.

Dividing the world into regions of similar faunistic or floristic composition and shared evolutionary history is a major aim of biogeography. The most prominent regionalization, Wallace's zoogeographic regions (*1*), has had tremendous influence, but its expert-based nature and lack of quantitative rigor and reproducibility have led to ongoing debates about the number and delineation of regions [reviewed in (*2*, *3*)]. In their Report, Holt *et al.* (*4*) follow recently developed methodology and results for mammals (*3*) and present a quantitative global regionalization that extends to birds and amphibians. Instead of pairwise turnover of species (or genera or families), they used the number of branches in variably resolved phylogenies shared between two assemblages. The integration of global range maps and phylogenetic information to delineate biogeographical regions is promising because it may overcome problems associated with mixed results reported from studies at the species, genus, and family levels (*3*, *5*). However, we believe that the key results of their study—i.e., an integrative delineation of the world's main biogeographical regions and the proposal of five new realms—are largely based on problematic data and methodology, as well as subjective decisions, and thus may have several conceptual flaws.

First, we are concerned about the overall poor and taxonomically and geographically disparate resolution of the tree topologies invoked. These were single trees in which only 40 to 60% of species were resolved, meaning that species' contributions to the regionalization were highly non-uniform and, in some cases, very minor.

Second, only counts of branches, not their actual lengths, were used for quantifying dissimilarity. This will in some cases equate species 20 million years old with those just 20,000 years old and ignores considerable differences in the ages of clades (e.g., amphibians versus birds) and regions. The authors suggest that in mammals,
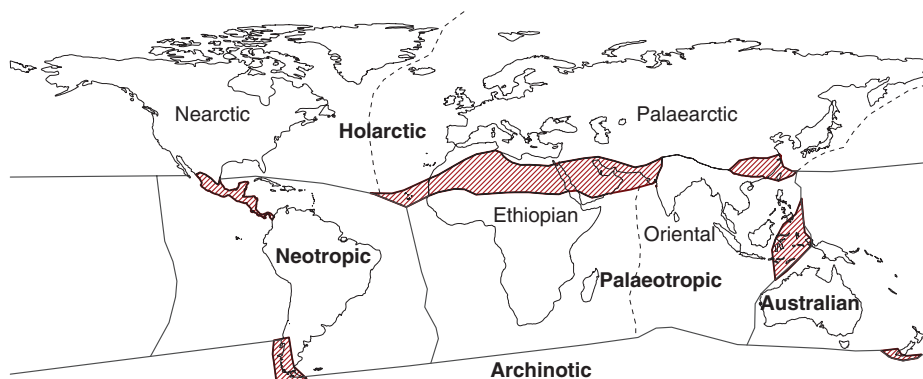
such differences, or even using just species' taxonomic separation instead, would not affect the existence and location of zoogeographic regions. We feel that this casts doubt, in this implementation, on the rigor and relevance of the "phylogenetic" method. New approaches are arising that account for all species in a single quantitative framework and that estimate branch lengths and uncertainty (*6*, *7*). In the midst of such major phylogenetic advances for vertebrates, we support caution over a rush in updating Wallace's regions.

Third, the authors propose the Saharo-Arabian, Sino-Japanese, and Panamanian as new "realms," even though they do not match their criterion of "phylogenetically distinct" regions (containing unique radiations and high degrees of endemism) but instead are well-known biogeographical transition zones where long-separated biota mix (*8*) and thus are of fundamentally different nature. In fact, there are striking similarities between these new realms and a map published 40 years ago that depicts biogeographical core regions as well as broad interjacent transition zones (*9*) (Fig. 1). For instance, it has been shown that the Saharo-Arabian is mainly an impoverished set of Afrotopical lineages, but with strong influences from the neighboring Palearctic and Oriental faunas (*2*, *10*). Similarly, the temperate-tropical transition zone in East Asia and Central America are regions of complex faunistic interchange (*11*).

We believe that raising transition zones to the rank of realms is inappropriate and will ultimately hamper biogeographical inference.

Hierarchical clustering identifies transition zones as distinct even if their distinctiveness results from mixing rather than independent evolutionary histories (Fig. 2). Applying clustering algorithms to biogeographical data is particularly challenging because the evolutionary distinctiveness of regions can be diluted by repeated episodes of faunal interchange (*8*). The unweighted pair group method with arithmetic mean (UPGMA) clustering algorithm used by the authors is unable to differentiate between the biogeographical core and transition zones, because transition zones will ultimately be merged with core areas with which they show the greatest affinity (compare Fig. 2D). In our hypothetical example (Fig. 2), the green region identified in the three-cluster solution is clearly qualitatively different from the black and red. Here, ordination plots of all grid cells are more informative in revealing how core regions are connected (Fig. 2C). As shown previously for mammals (*3*), a nonmetric multidimensional scaling (NMDS) ordination including all grid cells would likely have revealed such gradual transitions. The NMDS plots presented by the authors for 11 realms and 20 regions [figures S1 and S2 in (*4*)], however, cannot fully reveal the complexity of biogeographical transitions.

Fourth, there is only limited quantitative support for the status of the new realms. It is a great challenge to determine the number of clusters, and stopping criteria are necessary to identify the most informative parts of a clustering dendrogram (*12*). To this end, the authors inspected how an evaluation metric (percentage between-cluster $p\beta_{sim}$) changed with the number of clusters. Commonly, such plots are used to identify a "knee"—i.e., the point of maximum curvature, as a cutoff point. Holt *et al.*'s cutoff of 95% of global $p\beta_{sim}$ was chosen arbitrarily, and that value is definitely higher than the "knee" in their evaluation curves [figure S8 in (*4*)]. Importantly, an only slightly lower cutoff would alter the results considerably,

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Fig. 1. Map of animal realms with broad biogeographical transition zones highlighted in red [redrawn and modified from (*9*)]. Realm names in bold were taken from the original map; nonbold names have the rank of regions and were taken from an accompanying table.
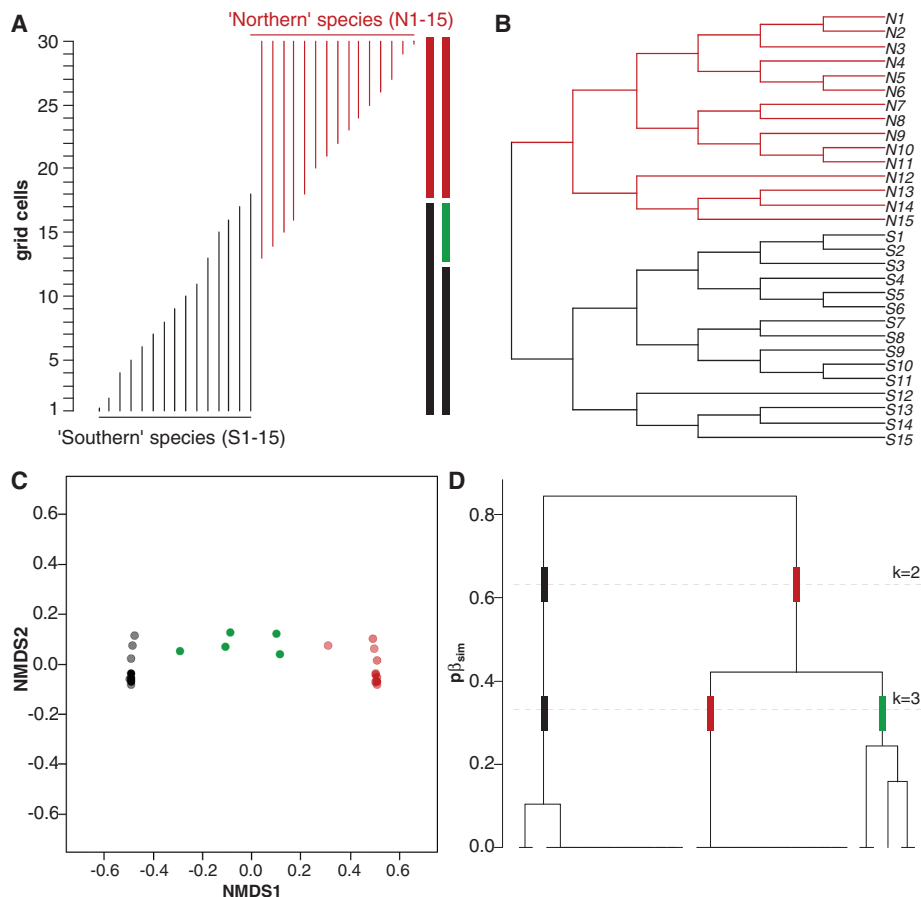
Fig. 2. Hypothetical example illustrating the performance of multivariate methods in a transition zone. (**A**) Two independently evolved species pools (black and red) blend into one another. Each thin line represents the distribution of one species. (**B**) Species' phylogenetic relationships. (**C**) A two-dimensional NMDS ordination solution based on a phylogenetic turnover ($p\beta_{sim}$) matrix based on the species distribution in (A) and the phylogenetic relationships in (B). (**D**) UPGMA dendrogram based on the same matrix. Horizontal dashed lines highlight two alternative cluster solutions, for $k = 2$ and $k = 3$. Red, black, and green color-coding of right-hand vertical bars in (A) and points in (C) signify UPGMA cluster memberships.

mine the number of clusters (*3*, *12*) would likely have produced different or mixed results.

In conclusion, given the intricate biotic interchange in space and time (*8*, *11*), biogeographers must be aware that expert- and algorithm-drawn boundaries are ultimately only arbitrary, although helpful, constructs that are inherently limited in fully capturing the biogeographical complexity. Regionalizations ideally should account fully for all species and their different evolutionary histories and require very careful interpretation. Promising alternative algorithms (*13*) and fully resolved and dated phylogenies are being developed (*6*), but until such conceptual and methodological issues have been resolved, a separation of new realms may seem premature.

References and Notes
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as the Saharo-Arabian would collapse into the Afrotropical, the Sino-Japanese into the Palearctic, and the Panamanian into the Neotropical—all resulting in currently recognized realm boundaries (*2*, *3*) that are largely consistent with Wallace (*1*). Alternative stopping rules or procedures to deter-