



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

Ben G. Holt *et al.*

*Science* **341**, 343 (2013);

DOI: 10.1126/science.1237541

---

*This copy is for your personal, non-commercial use only.*

---

**If you wish to distribute this article to others**, you can order high-quality copies for your colleagues, clients, or customers by [clicking here](#).

**Permission to republish or repurpose articles or portions of articles** can be obtained by following the guidelines [here](#).

**The following resources related to this article are available online at [www.sciencemag.org](http://www.sciencemag.org) (this information is current as of January 24, 2014 ):**

**Updated information and services**, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/content/341/6144/343.4.full.html>

A list of selected additional articles on the Science Web sites **related to this article** can be found at:

<http://www.sciencemag.org/content/341/6144/343.4.full.html#related>

This article **cites 13 articles**, 5 of which can be accessed free:

<http://www.sciencemag.org/content/341/6144/343.4.full.html#ref-list-1>

This article appears in the following **subject collections**:

Ecology

<http://www.sciencemag.org/cgi/collection/ecology>

Technical Comments

[http://www.sciencemag.org/cgi/collection/tech\\_comment](http://www.sciencemag.org/cgi/collection/tech_comment)

# Response to Comment on “An Update of Wallace’s Zoogeographic Regions of the World”

Ben G. Holt,<sup>1,2\*</sup> Jean-Philippe Lessard,<sup>1,3\*†</sup> Michael K. Borregaard,<sup>1</sup> Susanne A. Fritz,<sup>1,4</sup> Miguel B. Araújo,<sup>1,5,6,7</sup> Dimitar Dimitrov,<sup>7,8</sup> Pierre-Henri Fabre,<sup>7</sup> Catherine H. Graham,<sup>9</sup> Gary R. Graves,<sup>1,7,10</sup> Knud A. Jønsson,<sup>7</sup> David Nogués-Bravo,<sup>1,7</sup> Zhiheng Wang,<sup>1,7</sup> Robert J. Whittaker,<sup>1,11</sup> Jon Fjeldså,<sup>7</sup> Carsten Rahbek<sup>1,7</sup>

Kreft and Jetz’s critique of our recent update of Wallace’s zoogeographical regions disregards the extensive sensitivity analyses we undertook, which demonstrate the robustness of our results to the choice of phylogenetic data and clustering algorithm. Their suggested distinction between “transition zones” and biogeographic regions is worthy of further investigation but is thus far unsubstantiated.

Our update of Wallace’s zoogeographical regions of the world was based on detailed and documented information on the geographic distributions and phylogenies of more than 20,000 species of amphibians, mammals, and birds. Kreft and Jetz (1) suggested that we had not investigated the sensitivity of the emergent biogeographic patterns to variation in the type of phylogenetic tree, clustering methods, and analytical assumptions. Yet, these analyses were clearly indicated in the main text and explained in detail in the supplementary materials of our paper. Kreft and Jetz (1) thus failed to acknowledge that three of the four issues they raised were addressed explicitly in our study. Their point regarding the

potential inclusion of “transition zones” between zoogeographic realms is potentially interesting but was neither supported by our results nor a part of the analytical framework of our study. We respond to each point in turn.

Kreft and Jetz (1) criticized the resolution of the phylogenies used in our study but provided no empirical evidence to substantiate their claims. Naturally, there is variation among the vertebrate clades in the resolution of the supertree phylogenies. Kreft and Jetz (1) suggested that analytical methods could have been used to improve phylogenetic resolution. Although methods to resolve polytomies are being developed, it is unclear whether they provide any meaningful informa-

tion in biogeographic analyses or whether forcing resolution of polytomies induces systematic error (2). The previously published supertrees for amphibians (3, 4) and mammals (5) used in our analyses have been widely cited in comparative ecological and evolutionary studies. Our avian supertree was based on a transparent method using published phylogenies and DNA sequences—the same data underlying the avian supertree recently published by Jetz *et al.* (6).

Kreft and Jetz (1) noted that phylogenetic branch length was not incorporated in our analyses

<sup>1</sup>Center for Macroecology, Evolution, and Climate, Department of Biology, University of Copenhagen, 2100 Copenhagen Ø, Denmark.

<sup>2</sup>School of Biological Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK. <sup>3</sup>Quebec Centre for Biodiversity Science, Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, QC, H3A-1B1, Canada.

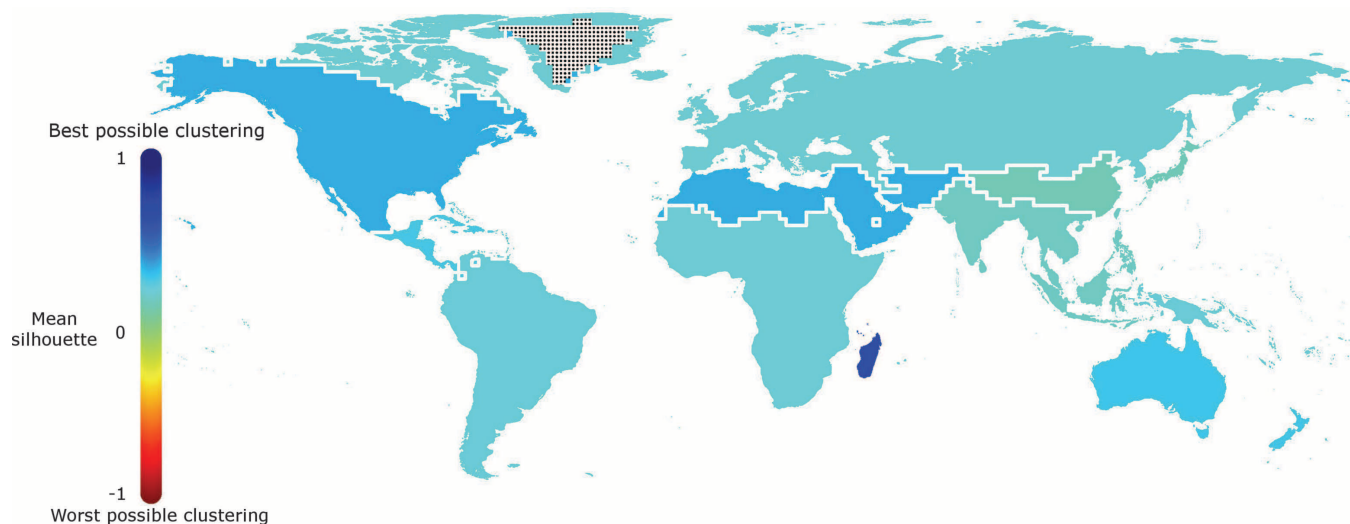
<sup>4</sup>Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt, Germany. <sup>5</sup>Department of Biogeography and Global Change, National Museum of Natural Sciences, Consejo Superior de Investigaciones Científicas, Calle José Gutiérrez Abascal, 2, 28006 Madrid, Spain.

<sup>6</sup>Centro de Investigação em Biodiversidade e Recursos Genéticos, Universidade de Évora, Largo dos Colegiais, 7000 Évora, Portugal. <sup>7</sup>Center for Macroecology, Evolution, and Climate, Natural History Museum of Denmark, University of Copenhagen, 2100 Copenhagen Ø, Denmark.

<sup>8</sup>Natural History Museum, University of Oslo, Post Office Box 1172 Blindern, NO-0318 Oslo, Norway. <sup>9</sup>Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794–5245, USA.

<sup>10</sup>Department of Vertebrate Zoology, MRC-116, National Museum of Natural History, Smithsonian Institution, Post Office Box 37012, Washington, DC 20013–7012, USA. <sup>11</sup>Biodiversity Research Group, School of Geography and the Environment, Oxford University Centre for the Environment, South Parks Road, Oxford OX1 3QY, UK.

\*These authors contributed equally to this work. †Corresponding author. E-mail: jplessard@bio.ku.dk (J.-P.L)



**Fig. 1. Map illustrating the performance of multivariate clustering of phylogenetic beta diversity (pβsim) values.** Mean silhouette values for eleven zoogeographic realms delimited in (2), calculated for each object where:  $s(i) = [b(i) - a(i)] / \max[a(i), b(i)]$ ; where  $a(i)$  = mean of pβsim values between grid-cell  $i$  and all other grid cells within grid-cell  $i$ 's realm,  $b(i)$  = mean of pβsim values between grid-cell  $i$  and all grid cells within grid-cell  $i$ 's neighboring realm (i.e., the most similar realm that grid-cell  $i$  does not belong to). Values range from –1 to 1, where positive mean values for a

realm indicate that objects within a realm are, on average, appropriately placed within that realm. “Transition zones” should have relatively low values. Our mean silhouette values presented in table S1 (2) are the most relevant to the transition zone concept and describe the relatedness of grid cells to their region, compared to the next best alternative; higher values indicate greater relatedness. For the hypothetical example of Kreft and Jetz, (1) the values are 1 and 0.89 for the black and red clusters, and 0.63 for the green transition zone cluster.

of dissimilarity among assemblages. At the time of our analyses, estimations of branch length existed only for the mammal phylogeny. We compared analytical results with, and without, the inclusion of branch length for the mammalian phylogeny, demonstrating that differences were negligible [see supplementary materials for (7)]. The inclusion of accurate branch length has the potential to facilitate finer delineations of regions within zoogeographic realms. However, our analyses of mammals suggest that the broad biogeographic picture is unlikely to change substantially. We also note that the dating of both the mammalian phylogeny (5) and the recently published dated avian phylogeny (6) has been questioned (8, 9). For example, 4 out of the 11 fossil calibration points used by Jetz *et al.* (6) were designated as being incorrectly identified avian taxa (8), which skewed the basal dating by millions of years and affected extrapolation throughout the supertree.

Kreft and Jetz claim that some of our realms do not match our criterion of phylogenetic distinctiveness because they are “transition zones where long-separated biota mix.” This argument is qualitative rather than quantitative and is unsupported by data or analyses. Kreft and Jetz (1) based their hypothetical example on a subjectively drawn map reflecting their perception of a data-poor map from 1973 (10). Our analytical results show little evidence of such a fundamental distinction between the realms identified as transition zones by Kreft and Jetz (1) and other realms. Our original figure 2 and table 1 indicate that the Sino-Japanese realm was indeed the least distinct of the 11 realms (see our original figure 1 for more details). However, the Panamanian and Saharo-Arabian realms, also highlighted as transition zones by Kreft and Jetz (1), exhibit distinctive-

ness that compares favorably with the other realms (Fig. 1). Although the distinction between two different types of biogeographic regions might be interesting and is perhaps worthy of further investigation (11), it was beyond the scope of our study and that of most other published, data-intensive, biogeographic regionalization studies (12–14).

Kreft and Jetz (1) argued that the “stopping rule” used to determine the number of meaningful biogeographic regions was arbitrary. There is a technical inaccuracy in Kreft and Jetz’s (1) comments. Although it is correct that our Saharo-Arabian realm would be merged into the Afrotropical realm if fewer realms were produced, this result would not be in accord with Wallace’s original map (15), as suggested by Kreft and Jetz (1). Most of our Saharo-Arabian realm falls within Wallace’s Palearctic.

The strength of our analytical approach is transparency. The full unweighted pair group method with arithmetic mean (UPGMA) cluster dendrograms allow individuals to choose their own cutoff points and set the number of regions/realms [see figure S1 in the supplementary materials in (7) for an example]. The rationale behind our choice of stopping rule was to select standardized evaluation criteria cutoff points (i.e., 95%, 99%, 99.9%), which explain a high level of variation in the data and can be used as conventional cutoff points for future comparisons. Kreft and Jetz (1) suggested using a stopping rule known as the “finding the knee” approach (12). This approach, when tested during the preliminary analyses of our study, proved unsuitable because it consistently produced results far from the point of maximum curvature on our evaluation plots (the intended objective of this analytical process).

In sum, in response to the concerns raised by Kreft and Jetz (1), we reaffirm that our analytical approach is transparent, repeatable, and broadly robust to the type and quality of data and to the choice of algorithm used to define biogeographic regions. We therefore refer interested readers to the supplementary materials of (7) for detailed illustrations of alternative regionalization solutions that can be produced using these methods and varying input data and parameters.

#### References and Notes

1. H. Kreft, W. Jetz, *Science* **341**, 343 (2013); [www.sciencemag.org/cgi/content/full/341/6144/343-c](http://www.sciencemag.org/cgi/content/full/341/6144/343-c).
2. T. S. Kuhn, A. Ø. Mooers, G. H. Thomas, *Methods Ecol. Evol.* **2**, 427–436 (2011).
3. S. A. Fritz, C. Rahbek, *J. Biogeogr.* **39**, 1373–1382 (2012).
4. R. A. Pyron, J. J. Wiens, *Mol. Phylogenet. Evol.* **61**, 543–583 (2011).
5. O. R. P. Bininda-Emonds *et al.*, *Nature* **446**, 507–512 (2007).
6. W. Jetz, G. H. Thomas, J. B. Joy, K. Hartmann, A. O. Mooers, *Nature* **491**, 444–448 (2012).
7. B. G. Holt *et al.*, *Science* **339**, 74–78 (2013).
8. G. Mayr, *Syst. Biodivers.* **11**, 7–13 (2013).
9. R. W. Meredith *et al.*, *Science* **334**, 521–524 (2011).
10. P. Müller, in *Biogeography*, P. Müller, Ed. (Harper & Row, New York, 1986), vol. 16, pp. 7–47.
11. P. H. Williams, H. M. de Klerk, T. M. Crowe, *J. Biogeogr.* **26**, 459–474 (1999).
12. H. Kreft, W. Jetz, *J. Biogeogr.* **37**, 2029–2053 (2010).
13. D. M. Olson *et al.*, *Bioscience* **51**, 933 (2001).
14. S. Proches, S. Ramdhani, *Bioscience* **62**, 260–270 (2012).
15. A. R. Wallace, *The Geographical Distribution of Animals* (Cambridge Univ. Press, New York, 1876).

**Acknowledgments:** We thank the Danish National Research Foundation for its support of the Center for Macroecology, Evolution, and Climate.

22 March 2013; accepted 14 June 2013  
10.1126/science.1237541