

## ECOLOGY

# A latitudinal gradient for genetic diversity

Within-species diversity of amphibians and terrestrial mammals is highest in the tropics

By **Henrique M. Pereira**<sup>1,2,3</sup>

**T**he tropics have by far the highest species diversity on Earth. Over two-thirds of terrestrial vertebrates occur in tropical moist forests (1). The species diversity is also highest in the tropics for several other taxa, such as vascular plants and arthropods, and in other realms, including freshwater and marine ecosystems. These latitudinal gradients were described decades ago (2), but recent work has yielded detailed knowledge of species-richness patterns. For example, Hurlbert and Jetz suggest that global maps of terrestrial vertebrate species richness are now accurate at resolutions of 100 to 200 km (3). Yet, little is known about the global patterns of genetic diversity. On page 1532 of this issue, Miraldo *et al.* help to fill this gap by presenting a global map of intraspecific (within-species) genetic diversity of amphibians and terrestrial mammals (4).

Many journals have required for years that authors submit sequence data to public databases. Miraldo *et al.* tapped into this resource to obtain more than 318,000 mitochondrial DNA sequences. However, not all these sequences could be used for a spatial analysis. Only 13% were georeferenced with explicit spatial coordinates. Another 30% had locality names. For the latter, Miraldo *et al.* assigned spatial coordinates to the locality names. Next, they grouped all usable sequences of a given species into ~400-km grid cells, ecosystems with different levels of human influence, and 10° latitudinal bands. They estimated intraspecific genetic diversity as the average number of variable nucleotide sites in the cytochrome B gene in pairwise sequence comparisons. Finally, they averaged the intraspecific genetic diversities across species.

The results suggest that for the two taxa analyzed, levels of intraspecific diversity are high in the tropics. However, whereas species richness declines almost monotonically away from the equator (1), genetic diversity seems to plateau around the equator (see the figure). This difference was not analyzed by Miraldo *et al.* and therefore will require further confirmation.

A possible limitation of the current analysis is the spatial heterogeneity in the data; in many tropical areas, the proportion of species sampled or the number of sequences are low. Furthermore, the authors gridded available point sequence data to estimate genetic diversity, in contrast to

some species richness maps, where individual species ranges are stacked to estimate species richness. In the former case, sampling effort can vary dramatically in neighboring spatial units. Addressing this problem will require harmonized efforts to sample genetic diversity in gap regions.

There is still a vibrant debate over what drives the latitudinal pattern in species richness (5, 6). Several explanations have been proposed for the higher diversity of the tropics. For example, higher climatic stability in the tropics may lead to lower extinction rates; higher evolutionary speed may result in higher speciation rates; and a larger surface area of tropical biomes over geological time may have led to a higher number of individuals on average and thus higher speciation and lower extinction rates. According to another hypothesis, greater energy availability in the tropics leads to larger populations. Biotic interactions can further cause positive feedbacks and reinforce the gradient. These mechanisms are not mutually exclusive and may all interact over time.

The high intraspecific genetic diversity in the tropics found by Miraldo *et al.* and other recent studies (7, 8) supports the evolutionary speed hypothesis, which is based on the idea that higher temperatures in the tropics lead to higher mutation rates. However, high numbers of mutations may also accumulate in large or stable population sizes over time (5). The influence of other drivers on the latitudinal gradient cannot, therefore, be excluded. Furthermore, intraspecific and interspecific diversity may interact in complex ways. For example, high species richness can increase intraspecific diversity as a result of increased competition for similar resources (9).

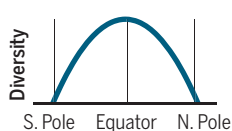
The total biodiversity at the genetic level of a region can be obtained by multiplying the number of species with the intraspecific diversity (see the figure). The resulting latitudinal gradient for total biodiversity is much more

## Latitudinal gradients of biodiversity

Miraldo *et al.* show that latitudinal gradients are similar for within-species diversity and for species richness. Multiplying the two components to obtain the total biodiversity curve produces a more pronounced gradient.

### Species diversity

Species diversity is highest in the tropics and declines with increasing latitude, reaching very low levels at the poles.



### Within-species diversity

The genetic diversity within species is also highest in the tropics but plateaus around the equator before falling off sharply with latitude.



### Total genetic diversity

The total genetic biodiversity is calculated by multiplying the species diversity and the within-species diversity. It peaks sharply in the tropics.



<sup>1</sup>German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany; <sup>2</sup>Institute of Biology, Martin Luther University Halle-Wittenberg, Germany; <sup>3</sup>CIBIO/InBIO, Universidade do Porto, Portugal. Email: hpereira@idiv.de

pronounced than for any of its components in isolation. The idea of total biodiversity as a multiplication of two components is also important for understanding the impacts of humans on biodiversity. A reduction of local species richness has been reported in several human-dominated habitats, although responses may differ across taxa (10, 11). Miraldo *et al.* found similar impacts at the intraspecific level, with amphibians showing lower genetic diversity in human-dominated ecosystems than in more natural ecosystems, although the response for mammals was not as clear. Therefore, reductions in species richness and genetic diversity caused by human activities have a negative synergistic effect on total biodiversity.

The study by Miraldo *et al.* has important implications for conservation. Protected areas have arguably been one of the most important tools for conserving the world's biodiversity. It remains unclear whether areas prioritized for conservation based on species diversity or even phylogenetic diversity (12) also capture intraspecific diversity. But perhaps the key question is how intraspecific diversity is changing over time in response to human drivers. This is an important societal question because Target 13 of the Convention on Biological Diversity for 2020 aims for the maintenance of genetic diversity. Moving from a single snapshot of the global distribution of genetic diversity to a dynamic map over time would allow major progress in answering this question. Such temporal studies will require advanced analyses, such as that by Miraldo *et al.*, but also improved geographical annotation of sequence data (13) and an increased effort to monitor global genetic diversity. ■

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Liu *et al.* use electrical resistivity data as a first-order proxy for the viscosity of the lithosphere beneath the Colorado Plateau. A two-dimensional model based on these results matches GPS and topography data.

#### GEOPHYSICS

## Constraining lithospheric flow

Geophysical data help to determine the viscosity of Earth's crust and upper mantle

By Boris J. P. Kaus

**T**he motion of Earth's tectonic plates—the lithosphere—is driven by the subduction of relatively cold and dense oceanic plates into the mantle. The resulting forces drive the motions of continental plates, but the manner in which this happens depends on the effective viscosities of the lithosphere and mantle. On page 1515 of this issue, Liu and Hasterok (1) discuss a novel method of constraining viscosities of the lithosphere from geophysical data.

Laboratory experiments on rock samples deformed under high pressures and temperatures show that viscosity is sensitive to many parameters, including temperature, stress, fluid content, and composition (2). Such experiments are necessarily performed at deformation rates much faster than actual geological processes. To apply the laboratory-derived viscosity laws to nature, they must be extrapolated over 10 orders of magnitude, introducing uncertainty. Moreover, it is unclear to what extent experiments on centimeter-scale samples are representative of the crust and lithosphere (3). As a result, the viscosity distribution of the lithosphere is one of the least certain parameters in geodynamics.

Alternative ways to determine viscosity on geological time scales are thus needed. A number of geophysical methods have been proposed, including postglacial rebound (4), geoid modeling (5), fitting global mantle-flow models to observed plate velocities (6), and postseismic relaxation studies (7). However, most of these techniques are sensitive to the larger-scale viscosity structure of the

mantle and not all that much to the viscosity structure of the lithosphere. In some areas, well-understood geological structures occur, such as in Hawaii, where the load of the volcano bends the Pacific plate, or in the Zagros Mountains, where the crust is folded in a regular manner. In those cases, comparison of computer model results with observations can help to determine the material properties of the crust and lithosphere in a more direct manner (8, 9). But these methods rely on having a good physical understanding of the underlying processes that formed these structures, which is only rarely the case.

Liu and Hasterok now propose a method that combines the results of magnetotelluric (MT) inversions with geodynamic models. MT inversions map out the lithosphere's electrical resistivity, which is sensitive to both fluid content and temperature. Making use of the fact that electrical resistivity and viscosity have a similar sensitivity to temperature, the authors propose a simple conversion factor to translate variations in electrical resistivity into variations in viscosity. Modeling of the Colorado Plateau (see the figure) shows that models with MT-derived lateral viscosity variations produce a much better fit to the GPS observations and topographies than do models without such variations.

This promising result suggests that MT inversion results give a first-order image of the variation of effective viscosities in the lithosphere, even though the magnitude of these variations needs to be calibrated with geodynamic flow models. Liu and Hasterok show that the use of nonlinear and brittle viscous-creep laws does not alter their basic conclusions. It remains unclear why electrical resistivity correlates so well with viscosity, but this relationship suggests that mechanically weaker zones in the lithosphere, which

Institute of Geosciences, Johannes Gutenberg University,  
D-55128 Mainz, Germany. Email: kaus@uni-mainz.de



Editor's Summary

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Henrique M. Pereira (September 29, 2016)

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