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commentary

Differences in climate and soil partly predict land use, population density, and conflict

In *The Wealth of Nations* (1776), Adam Smith argued that countries guided by the invisible hand of unencumbered economic markets would prosper, but he acknowledged that climate, isolation, and lack of access to rivers and oceans would hinder a nation's development. Jared Diamond's *Guns, Germs, and Steel* (1997) famously reinvigorated the consideration of how biogeographic variables have affected the fortunes of different world regions. Diamond argued that the size and orientation of Eurasia, together with its fortuitous endowment of climate, soil, and domesticable plants and animals, favored the earlier development there of agriculture, cities, and empires and that this "head start" affects economic fortunes to this day. Some studies support Diamond's hypothesis that biogeographic variables strongly affect economic development (e.g. Hibbs and Olson 2004; Presbitero 2006) and that the effects of the Neolithic revolution, the first agriculture revolution, still influence world incomes (Putterman 2008). Others argue that the "right" mix of *institutions*, meaning societal rules like property rights and competitive markets that influence behavior and economic incentives, internally promoted economic and technological development and were more important than biogeographic conditions (e.g. Acemoglu et al. 2002a; Easterly and Levine 2003).

Beck and Sieber (2010, PLoS One) extend Diamond's framework one step back, assessing whether climate and soil alone can predict the distribution of four basic land uses (agriculture, sedentary animal husbandry, nomadic pastoralism, and hunting-and-gathering), which reflect basic aspects of human cultural and economic practice. They then assess whether climate and soil affect population density, presumably through land use differences, and whether modeled regions of "overlap" in land use suitability predict locations of violent conflict. They focus on all but the Americas and Antarctica and divide this expanse into a 5km x 5km grid in a GIS framework.

The authors creatively adapt ecological niche modeling (Peterson 2001) to predict the geographic distribution of land use types based on the ecological distribution of climatic and soil conditions of a sample of sites of known land use, each site being a grid cell. In other words, knowing the ecological conditions of some places a land use is practiced, they predict where else it is likely to be practiced based on the presence of those conditions. The sample of land use types are records of locations, converted to grid cells, where that land use is currently practiced by a human society. They attempted to avoid spatial autocorrelation by using only a few records from each society.

The authors chose a maximum entropy (Maxent) variety of ecological niche model, often generally termed a species distribution model (SDM). Maxent estimates the most uniform, or *entropic*, geographic distribution of land uses subject to the constraint that the distribution of climatic and soil variable values among them must equal its empirical average from the sample sites (see Phillips et al. 2006).

To test their model's accuracy, they then a) compared its predictions of different human land use "niches" with actual presence records drawn from a variety of published sources, b) compared their model predictions to U.N. Food & Agricultural Organization records of actual agricultural practice, c) calculated an "index of shared (land use) suitability," and compared predictions with a database of post-1945 conflict data, and d) calculated regressions of the suitability for agriculture vs. log population density and suitability for agriculture vs. GDP-PPP, an index of economic strength.

Their findings support the hypothesis that the geographic template affects basic economic and political patterns of modern humans. The model was most accurate for predicting the presence of sedentary animal husbandry and least accurate for nomadic pastoralists, but it was fairly strong in general. It modestly predicted popula-

tion density and “economic strength,” explaining 38% and 16% of data variability, respectively. This suggests that in the modern world, population size and economic development are only partly hostage to traditional land use practices and their capture of different percentages of the land’s net primary productivity.

Like all null models, this one trades off accuracy and specificity for generality and explanatory power. For example, not necessarily focusing on “typical” site presence records (settlement areas) for included ethnic groups treats all the same and so is presumably unbiased, but “typical” settlement sites and associated land uses of given cultures are probably the best reflection of cultural adaptation to the logical land use available given climate and soil, just as the middle region of a species range or the areas of highest population density likely best reflects its niche in ecological space. Extending their findings to the Americas would provide an interesting test: because the Americas have been occupied relatively recently (about 15,000 years), similar findings might suggest a stronger role for ecology than for historical effects.

Perhaps unsurprisingly, deviations from model predictions were not geographically uniform. The model overpredicted agriculture versus FAO land use records, especially in southeast Asia, central Africa, and Central Europe. Interestingly, such overprediction is common to species distribution modeling generally because dispersal barriers, competition, and other factors restrict the realized niche to a subset of the fundamental (potential) niche (Phillips et al. 2006). The author’s wisely suggest that regions they predict should be more populated may be likely to “fill up” soon and so should be given conservation priority. However, the relative efficiency of maxent makes it more suitable for predicting the geographic projection of a land use’s realized niche (see Jiménez-Valverde et al. 2008). This suggests that the SDM method chosen may underpredict potential regions of use and, thus, regions worthy of conservation. In fact, the model does underpredict population density in India, China, Germany, and Britain. In India and China it underpredicts agricul-

ture, so more crops grown there support more people. In Germany and Britain, dense urban populations are partly supported by fossil fuel subsidies to agricultural productivity and to food imports. The model considers cities as “positive deviations from model expectations.” Geographic variables and features conducive to historic settlement, such as proximity to rivers and coasts and in protected valleys and natural movement corridors, might better predict population density by predicting city formation. Ultimately, the power of urbanization and industrialization, both real and imagined, makes Beck and Sieber’s findings all the more compelling: even in our hyper modern era, humans don’t just leave our footprints on the Earth; the Earth leaves a large one on us.

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Edited by Joaquín Hortal

commentary

Hot research on roasted lizards: warming, evolution and extinction in climate change studies

In volume 328 of *Science*, a team headed by Barry Sinervo published a study forecasting the effect of increased temperature in lizards. They demonstrate that climate change has already caused extinctions of lizard populations worldwide. They also forecast that if climate change scenarios come true, 40% of all lizard populations and 20% of all species could be committed to extinction by 2080. Predictions are supported by a model that represents how much activity time will be restricted (i.e., hours of restriction; hr) because operative temperatures are too high.

The study uses a multidisciplinary approach incorporating ecophysiology, evolutionary biology, biogeography and phylogenetics. A special strength of the study is that it uses models that are validated with data from recent population extinctions, which is an extremely rare feature in studies assessing climate change effects on biodiversity (but see Araújo et al. 2005). Sinervo et al.'s study links temperature increases to the organismal biology of the lizards making it possible to predict local extinctions. Unfortunately, such a link leads to a worrisome message: "Climate-forced reptile extinctions are happening now" (Huey et al. 2010).

Forecasts of species extinctions due to climate change are typically based on assessments of changes in climatic suitability for species (e.g. Thomas et al. 2004; Thuiller et al. 2005). Sinervo and colleagues go beyond this climate envelope approach and incorporate aspects of the ecology and behavior that are thought to mediate the re-

sponses of species to climate change. The incorporation of ecological and behavioral mechanisms into models attempting to provide insight of the likely responses of species to climate change is welcomed (Brook et al. 2009), but when such attempts involve large numbers of species and biogeographical scales compromises between precision and generality are inevitable.

One of such compromises is related to the use of estimated operative temperatures (the equilibrium temperature of a lizard with its thermal environment) in the study. Operative temperatures can vary greatly due to micro-environmental heterogeneity (Bauwens et al., 1996). Lizards may select locations with cooler micro-climates instead of moving higher in altitude or latitude. Open habitat species for example, may encroach into forests (Huey et al. 2009). This study would have benefited from integrating small scale thermal heterogeneity into large scale studies, although precisely how this can be accomplished remains a key challenge for mechanistically motivated models of climate change.

Investigators such as Kearney et al. (2008) and Mitchell et al. (2008) have created biophysical models of the thermal environment of reptiles to make predictions on the effect of global warming on individual species. These models use heat and energy balance equations to relate environmental conditions with ecophysiological traits measured in the laboratory. These relationships can be mapped geographically to evaluate climate suitability for the species of interest. Sinervo et al.