perspectives in biogeography

Hypothesis testing, curve fitting, and data mining in macroecology

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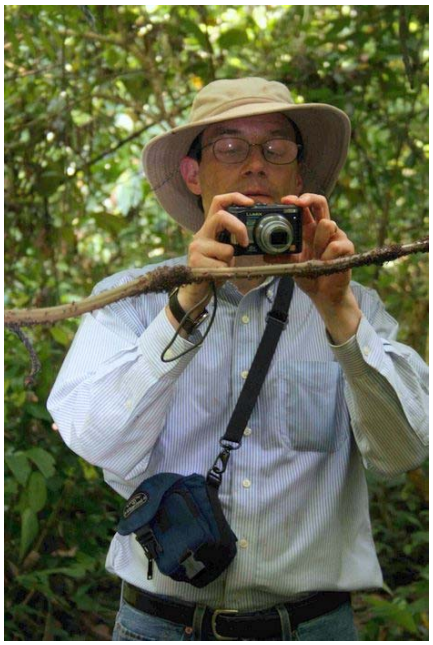
Changes in technology and methodology can have a big influence on how we do science. In this essay, I will discuss how new methods for the acquisition and analysis of data have affected biogeography and macroecology.

The underlying data used by macroecologists are geo-referenced specimen collections (GBIF 2008). For many decades, biogeographers explored the globe to collect and catalog these kinds of data (e.g. Darlington 1957). The numbers, usually counts of species or maps of geographic ranges, were plotted in simple graphs and used in support of narrative explanations and historical accounts of the patterns. Explicit hypothesis-testing was rare, although pioneering analyses of taxonomic diversity indices by C.B. Williams and other European ecologists (Järvinen 1982) foreshadowed the statistical perspective that would begin to dominate ecology and biogeography in the 1970s (Gotelli and Graves 1996).

Today, the widespread availability of compiled data sets on the internet means that young scientists can begin successful careers in macroecology without ever going in the field to collect data themselves. Of course, since most of the earth's biota has not even been described taxonomically (May 1995) – much less mapped biogeographically – there is still a great deal of primary data collecting to do. But even some of this activity may become automated, with the most promising avenue being the mapping of vegetation through the use of remote sensing and satellite imagery (Gillespie et al. 2008).

With less emphasis on data collection, more energy has gone into statistical analysis and interpretation. Sophisticated methods such as spatial regression analysis (Lichstein et al. 2002) have been used to compare patterns in multiple data sets and address long-standing



hypotheses about the origin and maintenance of the latitudinal gradient in species richness (Rohde 1992, Willig et al. 2003). An entire subdiscipline of bioclimatic niche modeling has emerged as macroecologists have used species occurrence data to predict how biotas will respond to global climate change (Elith et al. 2006).

In spite of this statistical sophistication, macroecologists still have not achieved a satisfactory understanding of global patterns of species diversity (Currie et al. 2004), nor have they developed trustworthy tools for forecasting future biotic change (Araújo and Rahbek 2006). In fact, the published conclusions still sound an awful lot like the narratives of the early biogeographers! But instead of making these arguments on the basis of simple species richness plots, macroecologists make them on the size of the *p*-values or the correlation coefficients from their regression models.

There are two related problems here, one with the hypotheses and the other with the statistical methods. For the most part, hypotheses in

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macroecology are just verbal descriptions of mechanisms ("higher productivity in the tropics allows for more biodiversity"). But since multiple explanations can generate the same qualitative patterns ("greater temperature stability in the tropics allows for more biodiversity"), we are not going to easily distinguish these mechanisms through qualitative assessment of correlations alone.

In this regard, I think the most important recent breakthrough in macroecology has been the development of metabolic theory (Allen et al. 2002). This theory, derived from first principles that do not depend in a circular way on existing data, predicts a quantitative relationship between temperature and biodiversity. Instead of just testing a null hypothesis of a slope of zero, we can now test whether observed slopes (with appropriate transformations) deviate from -0.65, the predicted value from the model (Hawkins et al. 2007). Controversy over the empirical support for metabolic theory (Hawkins et al. 2007, Gillooly and Allen 2007) should not obscure its importance: metabolic theory makes quantitative, not just qualitative, predictions and that is what we need right now in macroecology.

Theoreticians should step up to the plate and develop quantitative theories for other hypotheses in macroecology. As recently proposed by O'Brien (2006), the water-energy model may provide an emerging framework that will generate functional forms for water and energy variables derived from first principles of physiology and physical constraints imposed by the energetics of liquid water. For now, however, these models are either entirely verbal (Vetaas 2006), or they are derived from fitted regression functions that are specific to particular taxa, spatial scales, and continents (O'Brien 1998).

In addition to the development of new theory, we need to move beyond analytical methods that simply fit curves to data and test patterns against simple statistical null hypotheses. Some macroecologists are beginning to develop stochastic simulation models that include explicit algorithms for the origin, spread, and extinction of species in a bounded geographic domain (e.g. Storch et al. 2006, Rahbek et al. 2007, Rangel et al. 2007) These mechanistic simulation models (Grimm et al. 2005) have their roots in the mid-domain effect (Colwell and Lees 2000), a pleasingly simple explanation for species richness gradients that emerged from the random placement of contiguous species ranges in a bounded domain. This kind of modeling exercise raises its own challenges: how do we empirically estimate model parameters, and how do we explore the behavior of such a model over a potentially very large parameter space? But this simulation approach may allow macroecology to move beyond statistical correlations, and can serve as a nice complement to theoretical investigations. Simulation models may even provide quantitative predictions in cases where the mathematical models do not have a tractable analytic solution.

In a provocative essay in *Wired* magazine, Anderson (2008) speculates that one day traditional hypothesis testing will be unnecessary. Some data-mining enthusiasts believe that, with enough data, correlations will reveal mechanisms in comprehensive statistical models that encompass all possible data. I think the data miners are probably right. Exciting new work in computer science has led to very sophisticated "reverse-engineering" algorithms that have great promise for uncovering the functional form of relationships among correlated variables. These new iterative methods use data partitioning, automated probing, and snipping to sequentially modify and test underlying nonlinear functions with data-rich time series.

For example, Bongaard and Lipson (2007) successfully recovered the functional form of the movement of a pendulum using as input

the temporal series of spatial coordinates of a swinging pendulum. Their algorithm repeatedly "sampled" the data set from the most critical regions (where the pendulum was changing direction) and iteratively arrived successfully at the correct equations for motion.

Interestingly, the same methods were not so successful when applied to the famous ecological time series of snowshoe hare and Canadian lynx populations (Elton and Nicholson 1942). The algorithm did generate a pair of coupled differential equations (Bongaard and Lipson 2007). However, we know that the hare-lynx cycle is not caused entirely by coupled predator-prey interactions.

The problem, of course, is not the algorithm, but the limited data that it was fed. The time series of pelt records from the Hudson Bay Company does not reveal the critical observations of hare populations on islands in eastern Canada that cycle in the absence of the lynx (Keith 1963). The analysis also did not include time series on the secondary plant compounds in tundra vegetation, which accumulate under intense grazing and may be ultimately responsible for endogenous cycles of the hare (Keith 1983). And the model did not include time-series on snowpack depth or solar sunspot activity, both of which probably contribute to the regional synchrony of hare lynx cycles (Sinclair et al. 1993).

Without such "expert knowledge" it is easy to understand why the model failed. If those data inputs were provided, I think it is very likely the model would reveal the correct functional form of the relationships among hare, lynx, vegetation, and climate. But for now, the use of passive machine-learning algorithms applied to large data sets is an inefficient way to test hypotheses and make progress in macroecology. And given the pressing need to understand how biotas will respond to climate change, I am not sure we have the luxury of waiting for these comprehensive data sets to accumulate.

Nevertheless, the paradigm of machine learning seems to be the direction that much of the bioclimatic niche modeling research is going. If the goal of this research is to understand how biotas will shift in response to climate change, I think it is going to be much more fruitful if we combine it with an experimental approach. Experimental translocation of individuals beyond their current range boundaries (Hellmann et al. 2008) and experimental manipulations of abiotic variables to mimic effects of climate change on populations and communities (Harte and Shaw 1995, Suttle et al. 1997) are very powerful approaches. Experiments can provide realistic parameter estimates for bioclimatic niche models. Even simple models that are supported by experimental data will probably be more trustworthy than sophisticated models that are not.

In sum, the availability of large data bases, the emergence of quantitative predictive theories, and the development of new computational tools and simulation methods make this an exciting time to be studying macroecology. There are pressing applied problems of global climate change that we can address with these new tools and data. And along the way, perhaps we will even answer some unresolved questions in biogeography about species richness gradients.

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