

Defining and mapping vegetation types in mega-diverse tropical forests

Vegetation maps of tropical regions usually show just two or three vegetation zones in forested areas of the lowlands. Ecologists have been pretty good at distinguishing climatic (dry, wet, montane) or structural (deciduous, evergreen) formations in tropical forests, but distributions of species are still largely unknown, and it remains an open question how well climatic and structural classifications correlate with species' distributions. Today's concern about biodiversity and species extinctions suggest that forest classifications based on species composition are needed, along with quantitative information on how many species are shared between various vegetation types.

A series of papers by Tuomisto and colleagues¹⁻³ has recently described a multi-disciplinary effort to define forest formations in the Peruvian Amazon, using the best statistical tools and the broadest range of data available. Their results show how variable these uniform vegetation zones in the lowland tropics really are. Starting with a thorough understanding of geological and soil variation in the area around Iquitos, Peru, they established vegetation transects across edaphic boundaries, assembled tree inventories and analyzed satellite images.

The transects crossed from white sand into clay soils in one case, and ridges and valleys in another. Tuomisto *et al.*^{1,2} then carefully sought to distinguish vegetation-environment correlation against a background of spatially-autocorrelated species distributions. (Spatial autocorrelation is a major problem in vegetation-environment studies, and has nearly always been ignored in analyses of tropical forests.) Their results showed that plant communities were sharply differentiated on the white sand and clay, and on the ridge tops and valleys. Cluster analyses or ordinations produced similar groupings whether ferns, Melastomataceae or trees were used. Most striking was the way communities reappeared when a transect left one habitat, crossed into another, then returned to the first.

Tuomisto *et al.*¹ also showed correlations between vegetation and environment using tree plots spread over 10000 km² on either side of the Amazon River near Iquitos, using the same statistical care. Ordinations showed that white-sand vegetation was quite distinct, but with few samples, patterns within the pre-

dominant clay soils were not convincing. Further ordinations with more tree plots collected from a variety of sources showed clear separation of swamp and white-sand vegetation, but only weak evidence that tree communities correlate with soil nutrients on the clay soils (these are unpublished data that I was able to review; cited in the *Science* article¹). Since white-sand and swamp communities have long been recognized as distinct, these results are not terribly surprising. It will be more interesting when further samples on various clay soils in the area are available.

Next, the research team analyzed Landsat Multi-Spectral Scanner images from the same area, and reproduced several remarkable images³. Various swampy forests stand out distinctly, and the white-sand forests are clearly separable from forests on surrounding clay soils. Most intriguing are distinct variations that have never been noticed in ground surveys. For example, there is a straight boundary on the satellite image in an area just east of the Amazon river, south of Iquitos, that follows an old river terrace, suggesting an abrupt transition in the forest. Most striking is the dramatic difference in color on opposite sides of the Amazon, both sides being clay soils, again suggesting a major, undescribed change in forest vegetation.

Finally, Tuomisto *et al.*¹ describe an analysis of Landsat images over a much wider area of the Peruvian Amazon. The number of distinct colors in 448 sample transects from satellite images was counted, and the size of each color region was calculated. The results were used as an estimate of 'biotope' diversity, which appeared to be very high. The mean patch of homogeneous color was 4.6 km long in upland forest, and a total of far more than 100 biotopes was estimated for the region. This is a remarkable result, for it demonstrates quite convincingly that the forest vegetation within this uniform climate zone is highly heterogeneous. Tuomisto *et al.* and I do not agree, however, on the source of this heterogeneity. They conclude that most of the heterogeneity is based on edaphic and geological variation, based on results from Iquitos. But only a fraction of all the biotopes they record have been explored on the ground, and much of the heterogeneity may not be caused by soil and moisture variation.

An exciting – but difficult to assess – alternative is that unpredictable pest outbreaks, disturbances, limited seed dis-

persal and chaotic fluctuations lead to patchiness at large scales. Imagine a (hypothetical) habitat with no variation in edaphic or climatic conditions over a wide area that is home to several thousand tree species. Add tens of thousands of herbivorous insect and mammal species and fungal pathogens, some of which are capable of defoliating adult trees or destroying entire seed crops, and imagine that many of these pests are host-specific, while others are generalists. How stable, in either time or space, would this tree community be?

I suggest that clumpiness could be initiated in such a community through new speciation events, accidents of good recruitment, or large disturbances; mathematical results also suggest that heterogeneity can arise in completely homogeneous systems ('spatial chaos'⁴). Clumpiness would tend to persist for a long time because of limited dispersal: a species might become abundant at one locale and only spread slowly across the landscape. Evolutionary events among pathogens leading to newly virulent strains would also be highly unpredictable, and pests too have limited dispersal and might thus decimate a tree population in one area but not elsewhere. The community would never reach an equilibrium species composition at any scale of space or time. This view is an extension of the drift hypothesis⁵ or the carousel model⁶, coupled with results on chaotic fluctuations in metapopulations⁷. Satellite images of this community would show a mosaic of differently colored regions, despite no underlying environmental variation.

Adding environmental heterogeneity to the system would liven the scene. Some species would become precisely adapted to certain habitats, performing poorly on adjoining habitats. But unpredictable events coupled with limited dispersal could hide or blur environmental heterogeneity, as poorly adapted species might cross habitat boundaries under certain circumstances, and limited dispersal and long lifespan could keep them there for extended periods. In addition, there would be generalist species that perform equally in several habitats, further blurring the boundaries.

There are data consistent with the view that heterogeneity does not match environmental features in tropical forests. Kwan and Whitmore⁸ found that individual tree species occur patchily in south-east Asia, and are uncorrelated with soil features. Also, in our fully mapped 50 ha plot on Barro Colorado Island in Panama, many very patchily distributed species show no correlation between abundance and environment. Three clear examples are *Psidium anglohondurens*, *Inga pezi-zifera*⁹ and *Prioria copaifera*¹⁰ all abundant in some regions, absent from others and

uncorrelated with each other or with any edaphic features. Many populations in the 50 ha plot are also changing in abundance rather rapidly, some as a result of a 30-year period of lowered rainfall^{11,12}. Also, in Central Africa, locations of extensive stands of the tree *Gilbertiodendron dewevrei* are uncorrelated with any topographic, edaphic or climatic variables¹³.

No one can doubt that there is climatic and edaphic heterogeneity in tropical lowland forests. Indeed, this heterogeneity may be crucial in explaining the high tree diversity. But with so many species and so many unpredictable features, drift and chaos will dominate the system, and my prediction is that quantitative inventories of tropical forests that attempt to explain species composition will always find most of the variance in the 'error' term. This notion may bother some ecologists, but I find it an exciting prospect for future research. Mapping tree and habitat distributions will be complex (vegetation zones will be inherently fuzzy and difficult to define) but not impossible. The challenge is to tease out the importance of edaphic heterogeneity and biotic interactions against the backdrop of unpredictability.

Tuomisto *et al.*¹⁻³ have set out a research paradigm to take on this challenge. Many more ground inventories coupled with careful statistical analyses will finally

allow ecologists and conservationists to see detailed distribution maps of individual tree species, vegetation clusters and habitat zones in the tropical lowlands. Such species-specific information will be crucial in calculating extinction rates in megadiverse tropical areas, and in trying to reduce those rates.

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Evolution of development: molecules, mechanisms and phylogenetics

How do different species evolve different morphologies? In principle, we already know the answer to this question: alterations in organismal development produce the diversity of forms we see in the biological world, and it is the evolution of ontogenies that result in the diversification of morphologies. Significant details, however, continue to remain obscure. How do these developmental alterations occur, and what are the genetic bases behind variations in organismal *bauplans*? What new insights on morphological evolution can be gleaned from molecular analyses of developmental pathways? And can techniques in phylogenetic systematics and evolutionary genetics help us to understand the evolution of developmental patterns? Precise answers are just beginning to emerge as our understanding of developmental genetic mechanisms continues to expand. This was evident in a recent meeting entitled 'Evolution of Develop-

ment: Molecules, Mechanisms and Phylogenetics' sponsored by the Society for Developmental Biology and the National Science Foundation (20–24 September 1995), and held at the Bodega Marine Laboratory on the northern California coast (USA).

The meeting was opened with an address by Rudy Raff (Indiana University, Bloomington, USA), who reminded participants that early work in developmental biology focused on unraveling the evolution of animal body plans. Raff suggested that we are in the midst of the second marriage of evolutionary and developmental biology, remarking that paleontologists today are just as likely to discuss *Hox* genes as molecular geneticists are to talk about the Cambrian radiation. New trends in developmental biology also provide opportunities for phylogenetic research, a point stressed by Rob DeSalle (American Museum of Natural History, New York). Draw-

ing from examples on his work on *Drosophila* systematics, DeSalle noted that developmental studies have proven useful in dissecting aspects of character evolution and the direction of character change, as well as recognizing structural homologies. Gene expression patterns, DeSalle asserted, supply new landmarks within morphological features, providing greater resolution and even redefinition of complex characters. Moreover, the genetic basis of character development in *Drosophila melanogaster* enables us to understand the mechanisms that underlie character parallelisms and convergences in different dipteran lineages.

Beyond the fruit fly

In *D. melanogaster*, embryo differentiation is controlled by a series of maternal-coordinate, gap, pair-rule and homeotic genes, which establish segment polarity and identity in the insect body. Genetic interactions within the fruit fly embryo are fairly well understood, and workers have begun to ascertain systematically the extent to which these interactions are conserved in other insect or even arthropod taxa. Although some patterns of early development appear conserved between