deep-sea hydrothermal vent communities (C.R. Fisher, Pennsylvania State University, University Park, PA, USA) dominance by a single crustacean *Notidotea lacustris* of a sub-Antarctic island stream fauna (E.D. Edwards, Dept of Conservation, Invercargill, New Zealand); and numerous examples of exotic predators and herbivores driving community structure and ecosystem processes. One major challenge for habitat restoration and conservation management is the reduction of such dominant alien species, although, occasionally, native dominants must be also brought into check, as is the case for southern blackbacked gulls *Larus dominicanus* on Matiu-Somes Island in Wellington Harbor (New Zealand). In addition to the well-demonstrated utility of islands in the study of evolution and biogeography, islands could be good model systems for the study of the ecology and management of species dominance.

Human impacts

The impact of humans on fragile island biotas also appeared in many discussions. The consequences of extinctions, distortions of community structure, or the uncertainties of species and ecosystem restorations were explicitly or indirectly addressed by many speakers. Humans have a long history on Pacific islands, nearly 35 000 years in some Near Oceanic Islands. Only recently has the magnitude of the impact of pre-contact societies on island faunas been recognized[1]. Information accumulating from throughout the Pacific suggests that, in addition to their impacts on animals, those early societies also drastically transformed the ecosystems and landscapes of islands[2]. When we are better able to appreciate that impact, we will need to revisit island models.

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Global biodiversity patterns: from description to understanding

Jeremy Kerr

The Energy and Geographic Variation in Species Richness conference was held at the National Center for Ecological Analysis and Synthesis, Santa Barbara, CA, USA, from 12–17 March 2001.

Almost everyone knows that there are more species in the tropics than anywhere else on Earth. Ecologists and evolutionary biologists have expended huge amounts of energy assembling hypotheses that attempt to explain the existence of this pattern and to answer the broader question of why there is such spatial variability in species richness[1]. At the core of most of these hypotheses is the link between climate (particularly measures of energy) and species richness. The so-called 'species richness–energy hypothesis'[2], or more generally, the 'species richness–climate hypothesis', predicts that, as heat and water availability increase, so does regional species diversity. The empirical record includes many studies that strongly support this link, which is forged from analyses of insect, vertebrate, plant, marine and aquatic taxa across most of the world[3]. This is not to say that other factors are unimportant: habitat heterogeneity, for instance, is known to play a role in determining species richness gradients[4]. The Energy and Geographic Variation in Species Richness Conference was a far-reaching effort to assess global species richness patterns for as many taxa as possible and to determine why these patterns might exist.

The conference began with several presentations that defined the state-of-the-art for the conference theme, and a few are summarized here. Brad Hawkins (University of California at Irvine, CA, USA) began with a presentation on global patterns of butterfly diversity and followed up with another on global bird diversity. He demonstrated strong relationships between richness and both climate and habitat heterogeneity, respectively, based on structural equation modeling rather than traditional multiple regression analyses. David Currie (University of Ottawa, Canada) presented work partly by Anthony Francis, Attila Kalmar and Robin Mackey on global tree and bird diversity gradients on continents and islands and, strongly supporting the theme of the conference, demonstrated that these patterns are essentially predictable using simple, climate-based models. Jeremy Kerr (Canada Centre for Remote Sensing, Ottawa, Canada) showed that habitat heterogeneity predicts Canadian butterfly diversity just as well as do measurements of climatic energy. Kerr also showed that geometric null models of diversity in Madagascar are less able to predict species richness than are canonical climate-based models once pervasive habitat destruction has been considered.

Other delegates presented a meta-analysis of the shape of the diversity–productivity relationship (Gary Mittelbach, Michigan State University, East Lansing, MI, USA), conceptual foundations for a general diversity theory (Dawn Kaufman, University of Santa Barbara, CA, USA; John Turner, University of Leeds, UK; Richard Field, University of Nottingham, UK), or strikingly consistent patterns of the invasibility of oceanic islands among different taxonomic groups (Dov Sax, University of Santa Barbara, CA, USA).

Additional presentations gave perspectives on biodiversity patterns and community structure among riverine fish and snakes across several biogeographical domains and also demonstrated how evolutionary processes contribute to contemporary patterns of diversity (Jean-François Guégan, CNRS-IRD, Montpellier, France; and Thierry Oberdorff, Musée National d'Histoire Naturelle, Paris, France).

High-tech help for biodiversity science

Much new research on spatial gradients of diversity relies on remotely sensed or other

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digital data, and employs geographical information system (GIS) technologies. Delegates agreed that these high-tech systems improve on manual methods of measuring diversity or environmental gradients. Detection of land cover – and, by extension, habitat heterogeneity – is now possible and increasingly accurate across very broad geographical regions (Fig. 1). Land cover data can be used to generate high-quality models of net primary productivity or of other factors that are highly relevant to the study of spatial patterns of biological diversity. For the most part, however, patterns discovered through manual interpretation of paper maps are consistent with those found using remote sensing and GIS, but the former have a heavy cost in terms of analytical flexibility and power. The increasing need for high-resolution satellite data is making fluency with GIS and image processing tools a necessity for scientists pursuing this research.

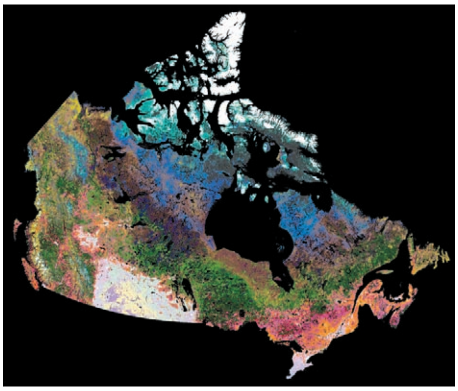

Fig. 1. A national land cover map of Canada derived from Advanced Very High Resolution Radiometer (AVHRR) satellite data from 1995. This research product identifies 31 major human-dominated and natural land cover types in Canada, ranging from boreal forest to high biomass agriculture. Analysis of data with such detail improves our ability to provide critical tests of diversity hypotheses; however, biodiversity data are rarely of comparable resolution. Reproduced, with permission, from Ref. 8.

Sharpening the cutting edge

During the conference, it was noted that much of the literature presenting new hypotheses that attempt to explain global biodiversity patterns ignores the impressive breadth of existing evidence[5]. This has led to the development of 30 or more hypotheses that could explain large-scale gradients in biodiversity. Many of these hypotheses are closely related to each other, but are treated as distinct. Similarly, some have been rejected repeatedly but continue to be cited as being equally probable as those hypotheses with consistent and strong empirical backing. Such issues lead to questions that should be answered by future work in this field:

Does the proposed hypothesis make stronger predictions than do competing (or existing) hypotheses?

Does the proposed hypothesis accomplish this parsimoniously (i.e. without invoking multiple 'exceptions-to-the-rule')?

Future studies must consider more than just one hypothesis at a time: positive evidence is easy to find (e.g. any variable that covaries with climate probably also correlates pretty well with regional species diversity), but this does not count as a definitive test of the hypothesis in question.

Predictions as a function of grain and extent

Keeping an open mind, therefore, delegates evaluated the predictive capacities of as many biodiversity hypotheses as possible at all spatial extents (geographical size of study region: from local to continental and global scales) and sampling grains (size of sample 'quadrats': meters to landscapes to regions). Studies with small sampling grains are much less likely to find strong relationships between, for example, elevation range and species diversity than are large sampling quadrats, because elevation usually varies only a little when grain size is small[6].

For several hypotheses with widely published support, a table of predictions was constructed that was categorized by spatial scale and geographical extent, respectively. The original batch of hypotheses was then ranked by expected importance. This provided a set of 'scaling behaviours' for the hypotheses. For example, it was thought that evapotranspiration, an integrated measure of heat and water, would be unimportant in local studies with small quadrat sizes, but might become progressively more important as the size of sampling quadrat and geographical extent of the study were increased. At continental and global scales, it was predicted that this factor, as well as others related directly or indirectly to climate (such as net primary productivity), would correlate strongly with diversity. Factors describing 'ecological' phenomena, such as competition, predation, or disturbance frequency/intensity were predicted to exert their most powerful effects on community structure, composition and richness at local scales and small spatial extents.

Efforts to predict the scaling characteristics of the focal hypotheses excluded direct consideration of whether these factors would exhibit a correlation of magnitude x with species richness independently of all other factors; this was, however, an underlying theme throughout these efforts. It is worth noting that latitude was never considered *per se* because it is meaningless as a biological variable, although the 'latitudinal gradient' persists as the unofficial moniker for the patterns that were discussed at the conference.

Fortified by the brilliant weather (from a Canadian's perspective), the delegates felt the meeting was a success. The question of why species richness varies so much across geographical gradients has been called the 'Holy Grail' of ecology[7]. Finding the grail will require broad collaboration, further acceptance of new scientific techniques and data sources, and renewed efforts to reconcile nearly two centuries of evidence from biogeography, ecology and evolutionary biology.

Acknowledgements

The conference was organized by Bradford Hawkins (University of California at Irvine, CA, USA) and Howard Cornell (University of Delaware, Newark, DA, USA). Josef Cihlar, David Currie and Brad Hawkins also made helpful comments on this report.

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