

New directions in biogeography?

Daniel T. Haydon

Brian I. Crother

Eric R. Pianka

The deduction of biogeographic process from the study of its history is complicated by the fact that history is a singular thing. This singularity allows no estimation of the degree of determinism surrounding the realization of biogeographic processes, and consequently we know almost nothing about the generality of such deductions. Here we discuss a new approach, called 'experimental biogeography', that exploits computers to model faunal build-up repeatedly against a fixed vicariant background over ecological and evolutionary time scales. This new approach enables a biogeographer to be omniscient – to know both vicariant history and actual phylogeny. Moreover, history can be replayed repeatedly to accumulate a sample of multiple phylogenies and to estimate probability density functions for biogeographic variables. Roles of stochastic, historical and ecological processes in adaptive radiations can also be assessed. Experimental biogeography allows examination of the reliability of various methods of recovering historical patterns.

Daniel Haydon is at the Dept of Zoology, Oxford University, South Parks Road, Oxford, UK OX1 3PS; Brian Crother is at the Dept of Biology, Southeastern Louisiana University, Hammond, LA 70402, USA; Eric Pianka is at the Dept of Zoology, University of Texas, Austin, TX 78712-1064, USA.

'What is history but a fable agreed upon'
(Napoleon)

The current diversity and distribution of Earth's biota constitute a single snapshot – one possible realization of a vast and ongoing probability experiment. The particular realization we observe has generated a variety of apparently non-random patterns (latitudinal gradients in species diversity, to name just one). Such

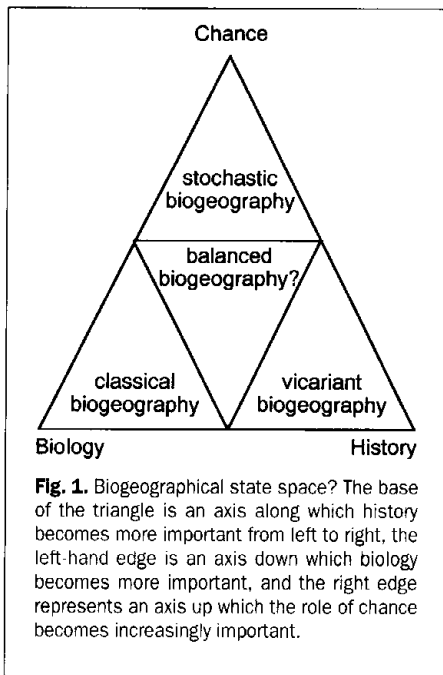
biogeographic patterns result from a long-term, auto-contingent sequence of dispersal, speciation and local extinction taking place over a continuous series of tectonic events. As in any other probability experiment, a spectrum of other possible outcomes exists, whose likelihoods are determined by some unknown probability density function. We have no conception of the variance associated with this density function, or where along it our current

result lies. We contemplate the output of just one simulation from what should be a full-blown Monte Carlo analysis.

Consider what insights access to such a complete analysis could yield. Regard tectonic and eustatic history over the past billion years as fixed and re-run the evolution of different taxonomic radiations hundreds of times. Alternatively, evolution of similar taxonomic radiations could be examined for their sensitivity to history. Suitably quantified, statistical models could be constructed, in which variance in outcome was partitioned into biology, history and error (chance). Error is a measure of the repeatability of the evolution of biodiversity, a quantification of the role of chance in the generation of biogeographical pattern. Biology, history and chance can be viewed as dimensions of a state space in which the biogeography of different taxa and regions may be plotted on a triangular plane in three-space (Fig. 1). Three regions of this surface are characterized by current foci of study: a corner associated with the concepts of vicariant or cladistic biogeography¹, another with classical centre of origin^{2,3} and island biogeography theory⁴, and a third in which generation of species distributions is dominated by the vagaries of stochasticity. The interior of this space defines a fourth region in which a consensus between these often conflicting perspectives may be sought.

Biology

Different types of organism (as might be assessed by vagility, life history strategy, extinction-proneness or generation



time) are differentially impressionable to the moulding force of history. For example, bats and spiders possess powers of dispersal that allow them to alter their distributions much more readily than can land snails or fossorial blind snakes. Therefore, the biogeography of bats and spiders confounds attempts to recover general patterns and responsible processes. Snails and blind snakes provide a better historical signal because they are less capable of altering the geographic distribution dealt to them by vicariant processes. In addition to such within-taxon processes, higher-order inter-taxonomic interactions (competition, predation, parasitism, symbiosis) probably influence the extent of adaptive radiations and ultimately may appear to be more deterministic over long time-scales. A possible example of such a deterministic result of these biological processes can be seen in the distribution of *Anolis* lizards on the Lesser Antilles. Different species occupying these islands always belong to different ecomorphs. There is never an overlap of type, resulting in some subset of one crown giant, one trunk-crown anole, one trunk-ground anole, one twig anole, and/or one grass anole⁵. Such distributions cannot be explained by vicariant processes alone, but result from biological interactions.

History

The extent to which a region's physical history is reflected in biogeographic patterns of its constituent taxa has been the focus of much recent attention⁶. The imprint of physical history on biogeographic pattern may vary for several reasons. (1) Additional information arising from biological dispersal-speciation

or anagenic evolution may dilute the historical signal (as observed for the biota of Jamaica⁷). (2) Local extinction processes may erode the strength of the signal (but may to some extent be recoverable through study of the fossil record). (3) The vagilities of taxa render them differentially susceptible to the varying scale of physical change (and therefore its accompanying tempo).

Different taxa within the same region may reflect the same physical history quite differently (e.g. honeycreepers and fruitflies in the Hawaiian islands^{8,9}). Additionally, the same taxa in different regions may respond dissimilarly if the scale of physical change is not the same (e.g. mainland versus West Indian iguanas). In sum, history's influence varies in its initial impact as well as in the extent to which it is subsequently attenuated.

Chance

Regional biogeographic patterns observed today are clearly the product of a long and spatially extensive interaction between biological attributes of the organisms present and the physical history of the region under consideration. One could argue that this interaction is technically deterministic, but on a practical level we will always remain so ignorant about details of this interaction that it must be regarded as stochastic. It would, however, be naive to assume that this interaction has been uniformly stochastic across all taxa and regions. We must therefore accept the likelihood that a varying fraction of any biogeographic pattern cannot be attributed to deterministic causes. Some stochastic processes have greater variances than others. Taxonomic radiations resulting from fundamentally different physical processes may permit a varying degree of stochastic influence. For example: 'epic' dispersal colonization events (e.g. Galápagos finches), vicariant fragmentation (e.g. ratite birds of Gondwanaland), eustatic or volcanic archipelago formation (e.g. Guayanan tepuis), 'accretion dispersal' (e.g. the collision of the Indian plate with Laurasia), or land-bridge emersion or submersion (the great American biotic interchange) may be differentially deterministic and thus map onto different areas in Fig. 1. Similar arguments suggest that a varying degree of determinism is present in dispersal and extinction processes associated with different taxa. If the signal of deterministic process is likely to run more clearly through the biogeography of some taxa or some regions than in others, some guidance to their respective whereabouts would be useful. Obviously, little can be learned from comparing largely stochastically generated patterns.

Inferring processes from patterns is difficult, and particular caution must be exercised when the sole existing pattern is the product of one realization of a process known to be unique and stochastic. Problems of spatial and temporal scale limit the role of empirical experimentation in the elucidation of these processes. Biogeographers have no choice but to undertake comparative work, using different fractions of the single existing realization. Global comparisons must be made between phylogenetic biogeographic patterns that differ widely in their underlying geophysical/eustatic development, or in the biology of their constituent taxonomic units, or both. At present, the different impacts of these phenomena cannot be controlled. Some guide to the significance of these considerations can be obtained through the use of experimental models of biogeographical processes.

Tactical approaches

Modern computers permit construction of highly detailed models of evolutionary processes acting over reconstructed sequences of tectonic/eustatic events. The hypothesized physical history of different biogeographic regions is programmed into a computer, and taxa allowed to roam over the evolving substrate, exposed to certain predefined stochastic processes of dispersal, speciation and extinction. Taxa are introduced that possess different (and non-evolving) vagilities, extinction-proneness, as well as other ecological attributes such as competitive ability. Experimental biogeographers are omniscient: a region's phylogenetic and biogeographic history is completely known. Moreover, repeatedly replaying faunal build-up against a fixed physical history allows statistical investigation of the influence of biology, chance and their interactions in the generation of biogeographic patterns. We have exploited this method to begin to investigate the variability inherent in biogeographical processes¹⁰. Sensitivity to uncertainties in physical history can be examined by introducing modifications to geographical development or eustatic history. General questions can be posed: radiations of taxa with different vagilities can be compared (Fig. 2), as can phylogenies of taxa with different extinction rates. Alternatively, specific questions can be addressed, such as: assumptions about initial distributions of particular taxa; importance of directional variability in dispersal, resulting from a current or prevailing wind; or the consequences of a proposed accretion or vicariant event. Through the use of such computer experiments, one can examine the sensitivity of biogeographic pattern

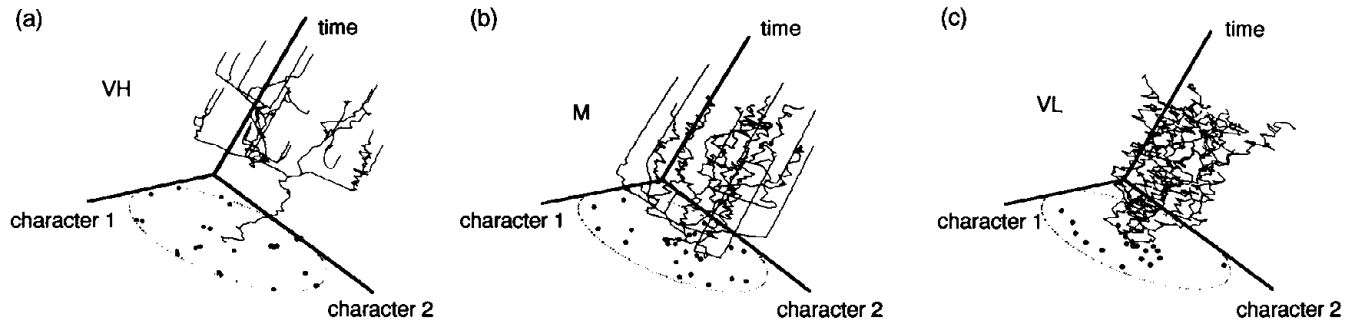


Fig. 2. Three phylogenies generated by a computer for three taxa with differing vagilities in the same hypothetical model archipelago. Niche space here is a two-dimensional circle depicted on the floor of the plots, with dots showing niche positions of surviving extant species: (a) taxon with a very high vagility, (b) taxon with medium vagility, and (c) taxon with very low vagility. Windows of opportunity for speciation for different taxa occur at different times in the development of the archipelago as islands drift apart, resulting in different clade structures and diversities. Highly vagile taxa do not speciate until relatively late in the archipelago's history when islands are far away from one another, whereas less vagile taxa speciate much earlier when islands are much closer together. *Redrawn from Ref. 10.*

to assumptions made about generating processes.

This approach can also be used profitably to test the accuracy and sensitivity of cladistic biogeographical techniques to various kinds of noise or to the reliability of different sorts of taxa in reconstruction of area cladograms – in much the same way that phylogenetic reconstruction algorithms have been tested against actual evolution¹¹ or computer-simulated data.

Strategic approaches

Another possible approach is to analyse moments of very simple probability models. For example, suppose that n different areas can be identified within one biogeographical region (A_1, \dots, A_n). The probability per extant species of a dispersal-speciation event between areas i and j is described as a function of inter-area distance, time, taxon, vagility, etc., and assigned to the ij th element within an $n \times n$ matrix \mathbf{D} . The number of species in each area is given by the vector \mathbf{S} . Area extinction rates per species are stored in a diagonal matrix \mathbf{E} , and the variance of the process

$$\mathbf{S}_{t+1} = (\mathbf{D}_t - \mathbf{E}_t) \mathbf{S}_t$$

(from time t to $t+1$) is analysed with respect to any parameters or conditions of interest. Suitably constructed, the \mathbf{D} matrix represents a variety of vicariant and tectonic processes, both simple and complex. Functions could conceivably be modified to accommodate additional complications arising from endemism and species-saturation effects.

The future

Both types of model suggest interesting problems with regard to what factors actually limit regional diversity or the size of radiations. Does regional geography dictate an upper limit to the number of species? If so, to what characteristics

of regional configuration is this limit sensitive? How well does realized diversity track this potential diversity ceiling over space and time? Large spatially homogeneous regions might have a lower diversity ceiling than highly complex archipelagos, but does diversity rise continually with ever increasing tectonic entropy? A great deal of speculation has been offered to explain the high species diversity in the tropics, but a large degree of tectonic or spatial splintering does not appear to be a necessary prerequisite for the generation of this higher diversity. Should we be suspicious of the role of allopatric speciation in the generation of diversity, or does our anthropomorphic perception of environments make us insensitive to the many subtle guises in which allopatry may be enforced? In interior Australia, a large radiation of skincid lizards (*Ctenotus*) may well have evolved by allopatric speciation caused by precisely such imperceptible mechanisms in a region commonly regarded to be highly homogeneous¹². Because the configurational integrity of the oceans is possibly more stable than that of landmasses, it would be interesting to know whether fundamental differences exist in features of the spatio-temporal development of terrestrial versus benthic and pelagic biomes and if this is reflected in differences in the overall biogeography of these biosystems¹³.

If an attainable diversity ceiling exists, chance may express itself through variation in the rate at which this ceiling is approached, or through variation in the manner and order in which primary resources are sequestered by evolving taxa. For example, how often does an adaptive radiation of one clade preclude diversification of another¹⁴? Interspecific competition and exclusion principles may lower this diversity ceiling, and may introduce elements of negative feedback to speciation, thereby reducing the influence

of chance on biogeographic pattern. However, a range of inter-trophic level processes (e.g. parasitism or predation) could have precisely the opposite effect. Currently, we know very little about the impact of such interspecific processes on diversity ceilings or vicariant patterns.

Scientists attempting to reconstruct phylogenetic or biogeographic history must acknowledge that history is a singular perspective that can only be estimated, never known. All but the most devout adherents of historical inevitability are thus confronted with a quandary: if conclusions to be drawn from the study of history are critically contingent on its accurate reconstruction, we are likely to be led astray by the vagaries of historical caprice. If conclusions are not critically dependent on history, then why do we labour so fastidiously over its reconstruction, other than out of our characteristic pedantry for descriptive detail? The merits of striving to establish the existence of mere historical fact might profitably be reassessed. An understanding of historical likelihood could prove to be a goal of greater conceptual value.

Asking interesting questions extends the horizons of scientific research. However, to progress toward these new horizons, such questions must be answerable. Hence, the best science results from inspecting or extending the intersection of sets of questions that are both interesting and tractable. Biogeography, and its prerequisite disciplines of phylogeny and taxonomy, currently enjoy the fruits of a biotechnological revolution. The tractability of questions raised here undoubtedly remains on the scientific horizon – but one that we feel may ultimately be accessible. As we frantically reconstruct estimates of the history of our idiosyncratic and singular 'realization', we might be wise to bear in mind the position of our particular trajectory through the historical state-space of all possible pasts.

BOOK REVIEWS

Acknowledgements

We thank Cliff Cunningham, Rod Page and Mitchell Leslie for reading and commenting on the manuscript.

References

- 1 Nelson, G. and Platnick, N. (1981) *Systematics and Biogeography: Cladistics and Vicariance*, Columbia University Press
- 2 Darlington, P.J. (1957) *Zoogeography: The Geographical Distribution of Animals*, Wiley
- 3 Wallace, A.R. (1876) *The Geographical Distribution of Animals*, Harper
- 4 MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*, Princeton University Press
- 5 Losos, J.B. (1994) in *Lizard Ecology: Historical and Experimental Perspectives* (Vitt, L.J. and Pianka, E.R., eds), pp. 319–333, Princeton University Press
- 6 Ricklefs, R.E. and Schluter, D. (1993) in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (Ricklefs, R.E. and Schluter, D., eds), pp. 350–364, University of Chicago Press
- 7 Crother, B. and Guyer, C. *Herpetologica* (in press)
- 8 Carson, H.L. and Kaneshiro, K.Y. (1976) *Annu. Rev. Ecol. Syst.* 7, 311–345
- 9 Williamson, M. (1981) *Island Populations*, Oxford University Press
- 10 Haydon, D., Radtkey, R.R. and Pianka, E.R. (1993) in *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (Ricklefs, R.E. and Schluter, D., eds), pp. 117–130, University of Chicago Press
- 11 Hillis, D.M., Bull, J.J., White, M.E., Badgett, M.R. and Molineux, I.J. (1992) *Science* 255, 589–592
- 12 Pianka, E.R. (1972) *Copeia* 1972, 127–145
- 13 McGowan, J.A. and Walker, P.W. (1993) in *Species Diversity in Ecological Communities* (Ricklefs, R.E. and Schluter, D., eds), pp. 203–214, University of Chicago Press
- 14 Duellman, W.E. and Pianka, E.R. (1990) *Annu. Rev. Ecol. Syst.* 21, 57–68