



## Conservation biogeography and the biodiversity crisis: a global problem in space/time

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'When the spatial model is hit upon, when it functions, critical reflection rests within it' (Derrida, 1978, p. 17).

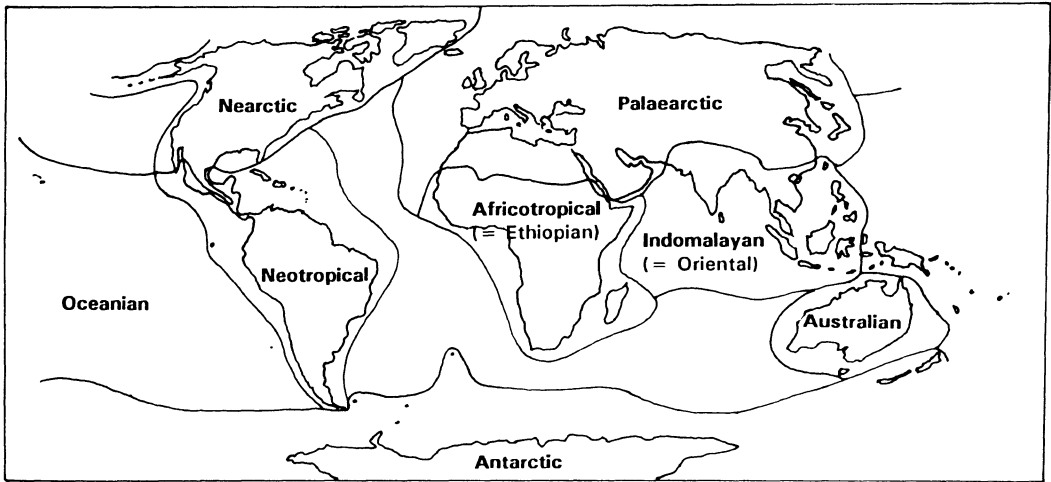
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The possible extinction of half of all terrestrial species over the next 50 years represents a potential biodiversity crisis of global dimensions. If a substantial proportion of the world's current biodiversity is to be retained, detailed studies of individual species will need to be replaced by methods that evaluate the conservation value of entire ecosystems (Ehrlich, 1992). To meet this challenge Ulfstrand (1992) called for the development of a research programme of 'space science magnitude' to document the patterns/processes characterizing biodiversity and develop tools for saving as much of the world's biodiversity as possible. The foundations for this programme may already be available in biogeographic concepts and methods. The geography of diversity is the subject of biogeography—the science of animal and plant distribution. Biogeography meets the 'space science' requirements of Ulfstrand (1992) because it provides methods to both document of patterns of biodiversity *and* understand the global biological and geological processes involved (Nelson & Ladiges, 1990; Grehan, 1992), although biogeography has not been funded at anywhere near a 'space science' magnitude.

Platnick (1992) recently observed that the biodiversity question is really a biogeographic one since it is a question of *where* on this planet should the limited financial and human resources be applied (Platnick, 1992). Different animals and plants occur in different places, and these differences are represented as the 'agony of choice' over setting conservation priorities (cf. Vane-Wright, Humphries & Williams, 1991; Crozier, 1992). If biodiversity was localized to a single point in space there would be no problem, but

in the real world different areas exhibit different levels of diversity and representation (Croizat, 1958; Platnick, 1992). Biodiversity analysis requires, therefore, a research and management programme with the conceptual and methodological tools capable of dealing simultaneously with a multitude of points or localities. Raven & Wilson (1992) proposed a 50-year data collection program to completely inventory all the global biota, but they acknowledge that this will do little, if anything, to address the loss of habitats such as tropical rain forests. Biogeography offers a cost effective alternative because global biodiversity information can be developed from available data without losing time and money on unnecessary exploratory research (Grehan, 1991).

During the 1980's biogeography became increasing sophisticated in methodology through new developments in panbiogeography and vicariance biogeography (Ladiges, Humphries & Martinelli, 1991). The expanded role for panbiogeography is due largely to research by New Zealand scientists on the conceptual and methodological foundations of panbiogeographic analysis (Craw, 1989; Heads, 1990; Henderson, 1990; Page, 1987). These developments provide analytical tools by which the geography of biodiversity may be understood in both the local and global context. Biogeographic systematics (vicariance cladists) recently questioned the convention that biodiversity is adequately represented solely by species richness or indices combining richness with abundance (Vane-Wright *et al.*, 1991; Williams, Humphries & Vane-Wright, 1991; Faith, 1992). They argue that biodiversity studies need to incorporate measures of taxic or



**Fig. 1.** The biogeographic classification system of Alfred Russell Wallace as modified by Udvardy (1975) to provide a global biodiversity classification under the International Union for the Conservation of Nature. Major modifications include the addition of 'Antarctica' and 'Oceania'. Note how some organisms, such as those of the mid-Atlantic and mid-Indian Ocean are not represented by any region at all.

phylogenetic diversity to maximise the preservation of total biodiversity. Current studies have focused on individual groups, but there are plans to investigate 'whole sets of faunas or floras' (Vane-Wright *et al.*, 1991). These systematic approaches are biogeographic in that they evaluate the phylogenetic representation of species occurring in different geographic localities, but the units of homology are based on the genealogical relationships of taxa, not their spatial relationships (Craw, 1983, 1985). However important the element of space, it remains *external* to the biodiversity concept and biogeography is relegated to describing an external space/time container within which the separate biodiversity elements reside. This presentation of biodiversity re-presents an organism/environment dichotomy in which space (environment) forms a fixed, immovable three-dimensional container within which objects/bodies (e.g. habitats, organisms) are embedded. Biodiversity is reduced to the separate universe of taxa passing through a separate category of absolute geological time and three dimensional space (cf. Craw & Page, 1988; Gray, 1990).

A methodological application of absolute space to global diversity was attempted by the International Union for the Conservation of Nature adopting a modified version of Alfred Russell Wallace's classification (Udvardy, 1975). The world was divided into a series of distinct regions or 'realms' (Fig. 1) that were to represent real biogeographic entities, or centres of

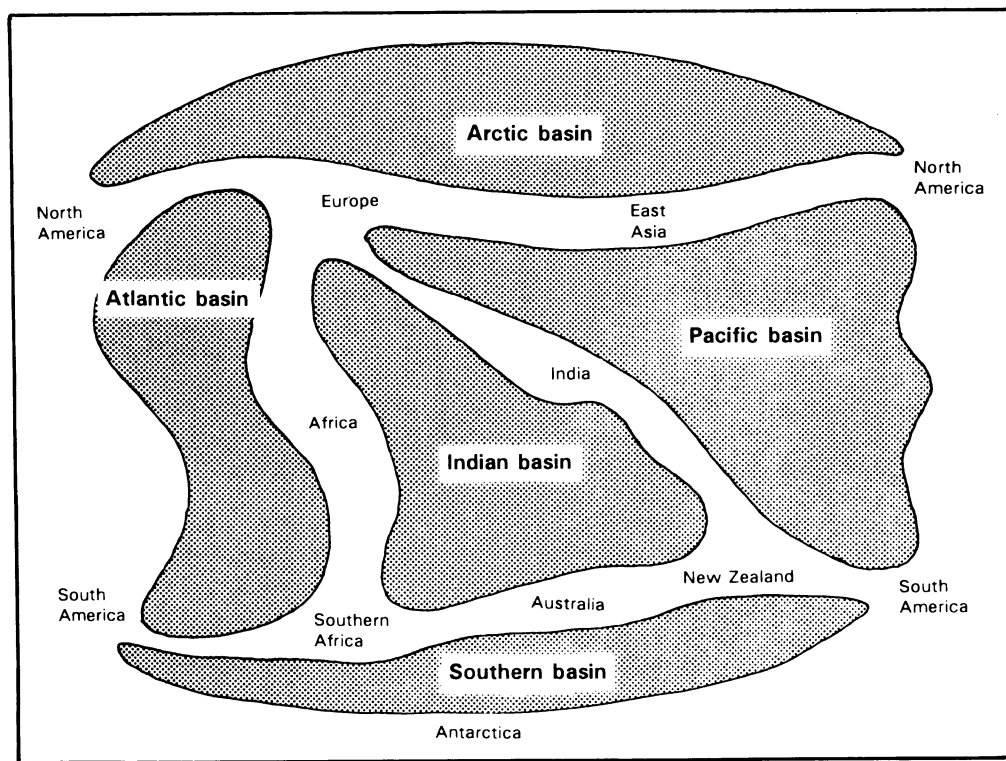
evolution, responsible for the present distribution of plants and animals throughout the world. The major regions comprised the larger containers or 'theatres of evolution' housing the different centres of origin for the evolution of the distinct biotic elements (Craw & Page, 1988). The Wallacean system is biogeographically problematic for conservation science because the units of classification—regions, realms, provinces—are defined by current geo-political boundaries. They do not represent natural entities, but are artefacts of current geography (Craw & Page, 1988). In conservation science the Wallacean system provided a descriptive context for local biological inventory (Grehan, 1991), but it did not generate new research methods or discoveries on biodiversity and appears to be largely irrelevant to current global concerns (cf. Eldredge, 1992).

For 'global biodiversity' to be anything more than a rhetorical slogan for conservation biology it must be recognized as an empirical reality—it is not possible to conserve something that has no real existence. The term ecology is widely acknowledged as a derivation of the Greek *Oikos* or 'house'—ecology is the literal metaphor for the study of organisms 'at home' (Odum, 1971). In panbiogeography the house does not constitute a separate container, but a process of relationship or *economy* which has its derivation from the Greek *Oikos* (=house), and *nemein* (=manage) (cf. Derrida, 1982, p. 4). This transliteration of 'house' to

'economy' is important to the biodiversity issue because metaphors orient research and fixes results (Derrida, 1978, p. 17). In the new biogeography the biodiversity 'house' is one of economy, both as a subject of study (of nature) and as a solution (of politics). The political consequences of separating organism and environment are manifest in New Zealand where biodiversity is locked away in a political container known as 'DoC estate'. This 'estate' resurrects a nature as a commodity (cf. Merchant, 1989) where the passive, subordinate elements are to be used and manipulated as a resource through conservation consultancies designed to raise capital as an end in itself. This subversion of biogeography represents a dislocation, from the economy of *Oikos* to an economy of *Oikesis* (the tomb) because without an economy of space/time, biodiversity is no longer focused on the landscape itself.

If biodiversity and biogeography are virtually synonymous, as claimed by Platnick (1992), the traditional

assumptions that separate space/time from the biodiversity 'elements' constitute a critical problem for conservation science. A relational concept of space/time is developed in panbiogeography where the Wallacean elements (organisms) and regions (environments) are synthesized under a new concept of biogeographic region and relationship (Fig. 2) (Craw & Page, 1988). In contrast to the static areas of the Wallacean system, panbiogeographic areas represent biogeographic homologies or baselines designating unique spatial relationships held in common for particular distribution patterns. The modern-day landmasses (Wallacean areas) are biogeographic composites (Craw, 1982). For example, the Nearctic (North American), biota comprises both Pacific (e.g. *Fagus*, *Magnolia*, *Equus*) and Atlantic elements (e.g. *Rubus*, *Erica*, *Boinae*). Major baselines are oriented to ocean basins because they represent global discontinuities in distribution patterns. The tectonic significance is evident from the presence on the ocean floor of



**FIG. 2.** Panbiogeographic classification representing ocean basins as the natural biogeographic regions from which present-day biotas are derived. The major landmasses occupy the position of biogeographic boundaries and are biogeographic (biological and geological) conglomerates. (Figure from Grehan, 1991.)

major tectonic features (e.g. spreading ridges) active in the earth's evolution (Croizat, 1964; Craw & Page, 1988). Novel geological predictions generated from this conceptual relationship have been corroborated by subsequent geological research (Craw, 1989).

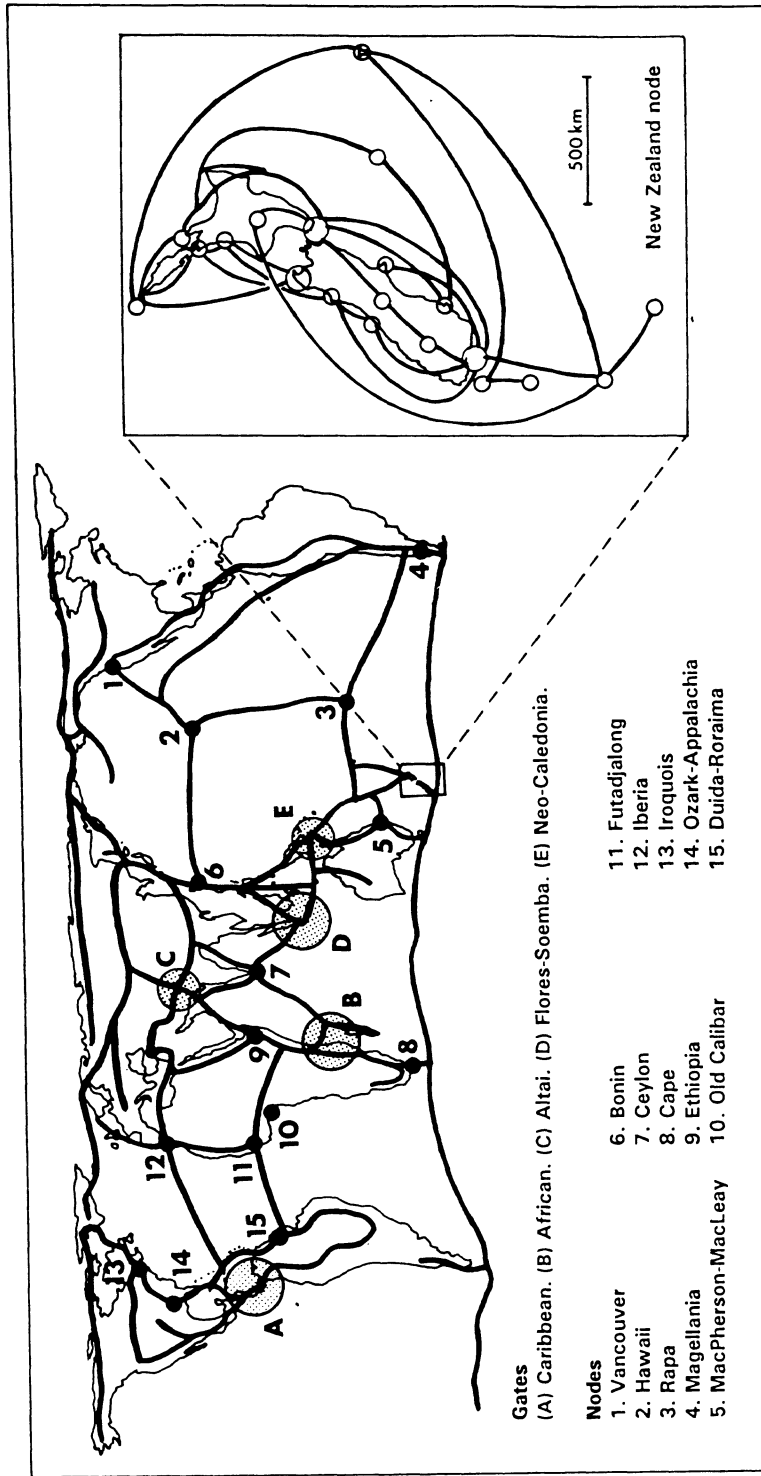
The panbiogeographic research programme represents the development of radically empirical biogeographic methods requiring analysis of raw locality data for taxa (Craw, 1989). Distribution records are converted into biogeographic patterns by connecting each disjunct locality to its closest geographic neighbour in the form of a line graph or 'track' (Croizat, 1964; Page, 1987). Points of intersection between different tracks are designated as biogeographic centres or 'nodes'. Track analysis is appropriate for biodiversity studies wherever taxonomic and distribution data is available. Croizat (1952, 1958) analysed track relationships using qualitative comparisons derived from an intimate knowledge of many different distributions. His approach provided a conceptual understanding of biogeographic structures and relationships, but it did not immediately provide quantitative or statistics procedures for track analysis. The quantitative requirement was first addressed by Page (1987) who linked track construction to graph theory and proposed the conversion of tracks into connectivity matrices. Pairwise comparisons of localities connected by tracks could identify nodes as localities exhibiting high connectivity values. Asymmetrical relationships between localities in terms of baselines could provide a method for comparing different tracks to each other and identifying those tracks sharing similar biogeographic orientation, even though they may not have an identical geographic overlap. Further comparisons could be carried out to distinguish between tracks with different biogeographic affinities, different ancestral distributions within the same overall track geometry, or the overlap of distinct tracks for organisms with locally congruent phylogenetic relationships. A similar approach was designed by Henderson (1990) who treated distribution points as track vertices. Nodal values could also be analysed by quantifying the number vertices representing distribution boundaries, and his analysis for New Zealand suggested correspondence with nodes derived from qualitative methods (cf. Heads, 1990; Henderson, 1990).

Croizat (1958) summarized global distribution patterns as a map comprising a network of standard tracks interconnecting nodes (Fig. 3). Standard tracks are composites of two or more tracks sharing the same baseline and imply the presence of general, non-random patterns common to organisms with different

ecological characteristics. A statistical analysis by Henderson (1990) suggested that the global pattern was well outside the 96% probability limits for a random distribution. Nodes are of particular importance for biodiversity research because they represent geographic localities where plants and animals may exhibit local presence (e.g. endemism), local absence (e.g. of groups found widespread elsewhere), diverse phylogenetic and geographic relationships with other areas, and the phylogenetic or geographic limits of taxa (Heads, 1990). Nodes provide an immediate geographic reference for centres of diversity because the combination of nodal characteristics comprise features associated with biotic diversity—nodes are 'biodiversity hotspots' in a biogeographic context. Croizat (1958) designated five nodes as 'gates' to denote their pivotal role in the evolution of current distributions. Many other nodes of global or regional significance are scattered over the globe and fifteen are identified in Fig. 3.

Each gate could provide a focus for the re-examination of global biodiversity. Biodiversity in the New World, for example, is centred on the Caribbean Gate which orients tracks to the north and south, across the Atlantic to Europe and Africa, and across the Pacific to Asia, the Far East and the South West Pacific. Nodes such as the Caribbean may include local diversity hotspots. Costa Rica (=Croizat's Nuclear Central America) and Galapagos, for example, are both in close proximity to the Caribbean Gate. The track/node network implies that the biogeographic (geological/ecological) events associated with the history of the Caribbean have influenced the disposition of ancestral distributions for much of the biota throughout North and South America. The conservation of natural biodiversity patterns involving local or regional concerns will be successful only by addressing the biotic patterns inside and outside the designated area of concern. Conservation of the Amazon patterns, for example, requires a conservation policy also for the Caribbean.

Natural biodiversity patterns in space/time cannot be conserved in isolation—conservation in isolation treats biodiversity as nothing more than an outdoor zoo or garden. The immediate problem for conservation science is how to develop policies to analyse local areas when the track/node network has no natural limits other than on a global scale. I suggest that the conservation of natural biodiversity patterns will have to start at the global level and work down to local and regional concerns through the representation



**FIG. 3.** The geography of global biodiversity represented as a network of tracks and nodes (modified from Croizat, 1958). Primary centres for biogeographic diversity represented by stippled circles (Gates). A selection of other regional diversity centres and relationships summarized for the New Zealand archipelago (from Heads, 1990).

of tracks and nodes. Croizat's (1958) bio-geodiversity map could, for example, provide an effective foundation for a biodiversity programme generating rapid results at a low financial cost compared with inventory programmes such as that of Raven & Wilson (1992). Inventory is a necessary continuing component of biodiversity studies, but may be most effective if targeted to specific problem localities where additional data can be effectively incorporated into an analytical programme. The 1988 panbiogeography symposium at the National Museum in New Zealand, for example, resulted in the first comprehensive summary of New Zealand's biogeographic resources with documentation of standard tracks and nodes that are closely correlated with major tectonic features involved with the Mesozoic origins and evolution of New Zealand (e.g. Heads, 1990) (Inset, Fig. 3). This model will form the conceptual core for a proposed research program, called the panbiogeographic atlas project, to catalog and synthesize distribution information from monographs, revisions, and collection data\*. The scope of data coverage and cost effectiveness of the programme will save millions of dollars over current methods in New Zealand (Grehan, 1991, 1992) and has major implications for conservation management policy by introducing new perspectives for evaluating local areas (Grehan & Climo, 1992).

Track and cladistic methods represent complementary applications of graph theory, each with their inherent limitations and advantages. Track methodology identifies relationships of taxa in terms of spatial geometry while cladistic approaches have focused on genealogical relationships between areas in terms of taxa. At a global level cladistic studies defining areas using non-biogeographic criteria and have produced results similar to those of Wallace (Craw, 1983), but this problem could be avoided if cladistic methods were applied to biogeographic units represented by tracks and nodes. Some cladistic authors have attempted to incorporate panbiogeographic findings (Ladiges, Humphries & Martinelli, 1991), but the exploration of systematic biodiversity remains comparatively isolated. In terms of complementarity, tracks represent spatiotemporal homologies that could be further investigated for their taxonomic representation through cladistic analysis. For example, how are phylogenetic patterns associated with particular nodes and tracks?

(Craw, 1989). Differences in phylogenetic representation, such as taxonomic dispersion, may provide indicators of nodal characteristics such as the boundary limits of taxa, relictual centres, 'unique' endemics, and the absence of important groups.

Biogeography is the 'spatial model' for biodiversity that provides empirical evidence for a 'global biodiversity' structure (tracks, nodes) in the real, natural world. This structure implies a new perspective for critical reflection in biodiversity where the ecological environment is no longer presented as a separate container enclosing separate elements (organisms), but as a new structure that is neither organism or environment alone, but both as localities in series—the track.

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