PROBLEMS WITH SMALL ISLANDS

by J. D. HOLLOWAY

ABSTRACT. Palaeogeographic maps are of great use in the biogeographic study of immobile terrestrial organisms, but less so when more dispersive groups are considered. Though the centres of evolution of more mobile organisms tend to be found on the larger land masses, they often interact and overlap along linking chains of small islands not assessed in palaeogeographic reconstructions. Analysis of such interaction requires further information on island arc formation at plate boundaries, good data on the current distribution of organisms, and a coherent, testable theory on the ecological and evolutionary development of biotas. These problems are discussed with reference to the Australasian biota and to the biogeography of New Caledonia and Norfolk Island.

INFORMATION on the past distribution of large land masses is of great use in the study of the biogeography of landbound terrestrial groups. In more dispersive groups the main centres of evolution are usually found on the large land masses but the interaction between such centres may create complicated patterns of overlap along connecting archipelagos. This is especially true of Australasia, linked with Asia and South America by island chains thrown up by the interaction of compressive plate boundaries. To investigate such situations, to define the origins and dispersal of various elements of fauna and flora, one needs detailed information in three areas. First a comprehensive, testable theory for the ecological and evolutionary development of biotas is needed to interpret patterns of distribution. Secondly the small-scale effects of plate tectonics at plate boundaries need investigating to provide information on the uplift, extent, and destruction of island chains. Thirdly, data on current distributions of plants and animals must be collected in a manner suitable for subsequent numerical analysis. Palynological information is also of great importance.

THE ECOLOGY AND EVOLUTION OF BIOTAS

Biogeographic patterns can be said to develop through the interaction of dispersal factors and the process of evolution with irregularities in the environment, past and present, geographical and ecological.

The study of dispersal is hampered by the inability to measure it actually happening. Levison *et al.* (1968) have developed a computer technique to synthesize dispersal phenomena, given information on seasonal wind direction, ocean currents, and survival values for the organisms concerned. This is a more practical approach than the theoretical modelling of MacArthur and Wilson (1967) which becomes complicated when applied to actual situations with seasonal variation in the agents of dispersal. However, the computer synthesis may provide means for testing the models.

The most encouraging approach to the study of evolution at the level of the community and biota is the analysis of environmental diversity. This is measured by studying the distribution of abundance amongst the species of a taxonomic

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group in a given community. I had cause to assess the literature on this subject in a thesis (Holloway 1970*b*, chapter 1) and came to the following conclusions.

Investigations in the literature of species/abundance curves for a wide range of plant and animal groups suggest that Preston's (1962) log-normal type curve gives the best fit. Numerical methods of analysis of quantitatively collected data facilitate the study of these curves by eliminating the effect of large environmental irregularities and consequent additive effects of curves with different properties. This will be illustrated later by curves derived from altitude elements in the moth fauna of Mt. Kinabalu (Holloway 1970*a*).

The properties of the log-normal type curve may indicate how evolution progresses in an interacting community of species. The curve is logarithmic, it encloses an area, and has a standard deviation. The area indicates the richness, the number of species in the community, and the standard deviation is a measure of the equitability with which individuals are distributed amongst the species. Richness appears to be related to the geographical area occupied by the community except in unsaturated areas where dispersal and time factors have prevented them from 'filling up' with species. Equitability increases both with saturation and with ecological succession, hence it will tend to stabilize as the community becomes ecologically mature.

Text-fig. 1 shows three species/abundance curves of high altitude communities in the moth fauna of Mt. Kinabalu in the island of Borneo. The log-normal curves of Preston can be derived by plotting the slope of the sigmoid with relation to the vertical axis. Kinabalu reached its present altitude in the Pleistocene and the fauna of higher altitudes is of recent derivation, isolated, and therefore unsaturated. The fauna of medium altitudes is less isolated, more saturated. The three curves illustrate increasing richness and equitability as one passes from the second highest element (2) to the lower montane element (4).

Fisher (1930) suggested that, as mutation occurs randomly, those species with a greater number of individuals will receive more favourable mutations than those with fewer individuals. Abundant species would expand at the expense of rare ones which would eventually become extinct. Fisher suggested that the total number of species in the community would be maintained by the fission of the more abundant species. MacArthur (1960) indicated that such a process would lead to a logarithmic species/abundance curve, the equitability being determined by the balance between the differential growth of abundance and the fission of more abundant species.

Brown (1958) wrote of genera and species groups normally containing potent, abundant species in which general adaptation is prominent, acting as 'apical growing points' of general adaptation, continuing the evolutionary line most likely to give rise to new major groups. Adaptive radiation and specialization provide a lateral component to the process, the fission of abundant species of Fisher. Darwin (1859) noted that abundant species tended to be found in more polytypic genera and to have greater variability and ecological amplitude than rare species.

Thus evolution may be a dynamic progression within the species/abundance relationship, richness gradually increasing as the biota develops greater efficiency from general adaptation at exploiting its environment. Variations in equitability would appear to be short term and could prove useful indicators of historical events.

Species ranked in order of abundance
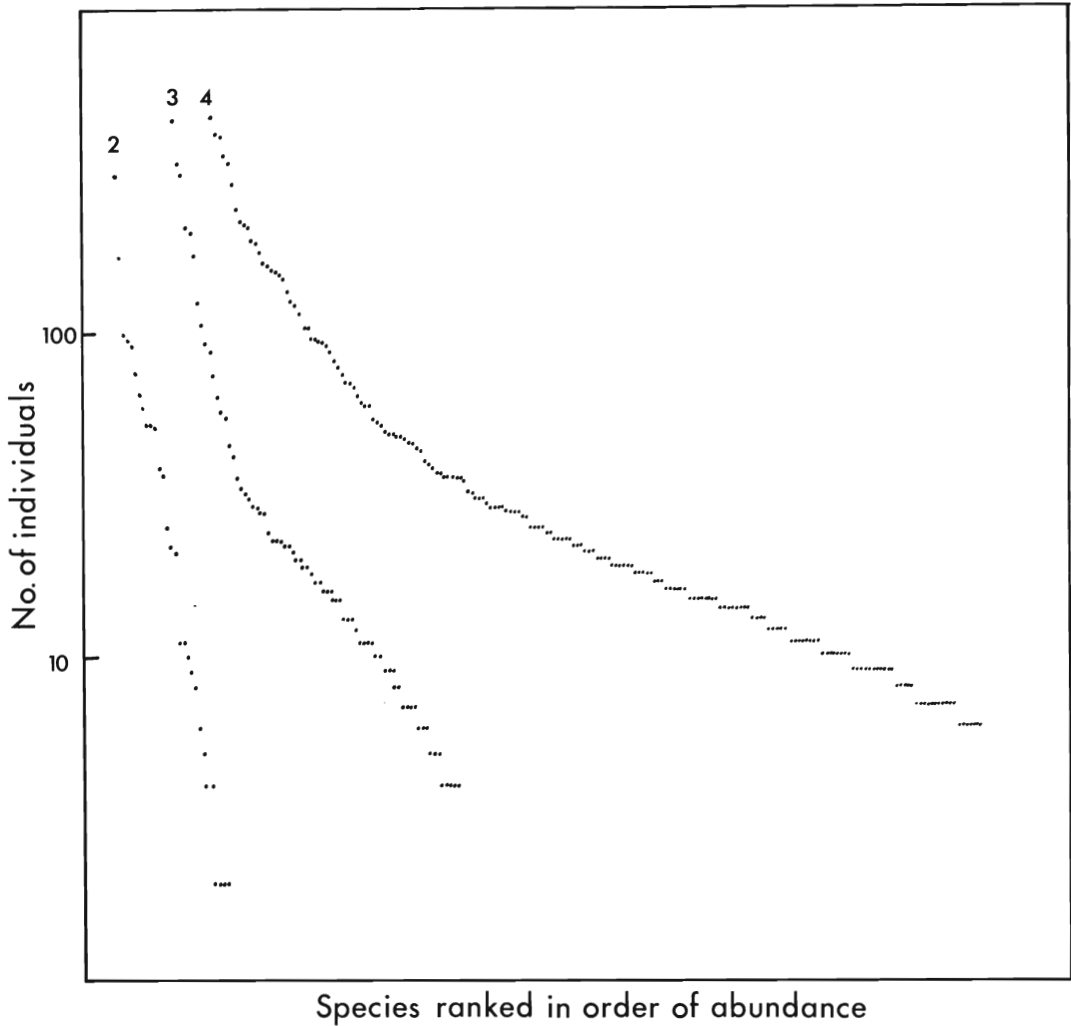
TEXT-FIG. 1. Species/abundance curves for altitude elements of the moth fauna of Mt. Kinabalu as derived in Holloway (1970*a*). (2) Radio Sabah element; (3) Upper montane element; (4) Lower montane element.

An ecological theory on this basis is open to mathematical development and can be used to approach more specific ecological and biogeographical problems. MacArthur and Wilson (1967) gave an indication of the value of such an approach in their book on the theory of island biogeography, islands providing the investigator with whole communities in microcosm. For example the observation that interchange between islands is primarily from the larger to the smaller can be predicted from the theory described if the community of the larger island be considered as an abundant species interacting with a less abundant one.

PALAEOGEOGRAPHICAL PROBLEMS

It follows from the ecological theory described that the larger land areas have always supported the main centres of evolutionary development. During the Late Cretaceous the major Australasian centre of development for the southern flora became isolated by the opening of the southern Indian Ocean. Thereafter interaction with other centres was only possible along chains of small islands extending to south-east Asia and South America. It is probable that the radiation of most of the families of the Lepidoptera coincided in the tropics with the development of the modern angiosperm flora after the isolation of Australasia. Thus most of the Australasian Lepidoptera would have been derived by dispersal along one or other island chain from centres in south-east Asia and South America. Therefore biogeographers working in the area are concerned mainly with problems such as the following.

Was there ever a spreading ridge in the Tasman Sea as suggested by van der Linden (1969) or has Australia moved north from proximity to the Lord Howe Rise as expressed more recently by Veevers *et al.* (1971) and Jones (1971)? Was there, in the Early Tertiary, more extensive land between New Zealand and New Caledonia along the Norfolk Island Rise, perhaps resembling the Japanese island chain as it exists today? To what extent did this archipelago continue through what is now northern Indonesia to the Philippines and mainland Asia at times in the past? Has the plate boundary through Melanesia and Indonesia always been in its present position or has it always been relatively close to the north of Australia? Further north the geographical history of Celebes presents problems. Though close to Borneo now, biological links between the two are recent, older links occurring between Celebes and the Philippines.

With such information it might be possible to clarify ideas on phytogeographic problems such as the history of *Nothofagus* in the Southern Hemisphere and the history of the spread of southern genera such as *Dacrydium*, *Phyllocladus*, *Agathis*, and *Leptospermum* north into Indonesia and south-east Asia. The distribution of butterflies presents similar problems. Three species of the primarily Holarctic genus *Chrysophanus* occur in dramatic isolation in New Zealand. Throughout Australasia are found widely divergent genera of the Satyridae, usually endemic to a single land mass, associated together at the tribe level as the Hypocystini by Miller (1968).

More specifically in New Caledonia there are contrasting relationships in the older floral elements with New Guinea and New Zealand on the one hand and with Australia on the other (Thorne 1965). Lillie and Brothers (1970) drew attention to the strong stratigraphical relationship between New Caledonia and northern New Zealand, but any such geographical relationship is liable to be confused by climatic changes in the Tertiary. Burbidge (1960) referred to a polarization of a uniform Australian flora into tropical and temperate elements. A similar polarization in the New Zealand–New Guinea chain might present the biogeographer with confusing latitudinal correlations.

At present one can only hope to unravel the history of the area through a process of reciprocal illumination between known biogeographical factors and known geological events. The harmony and endemic development of the part of the New Caledonian flora of southern affinities suggests a long period of uninterrupted and isolated

development. The adaptation of this southern element to mineral-rich, lateritic areas resulting from the destruction of serpentine may indicate that New Caledonia has enjoyed a long association with the western margin of the Pacific Plate, as serpentine extrusions are generally associated with compressive plate boundaries. One may contrast the situation in New Caledonia with that in Norfolk Island to the south, of recent volcanic origin, composed mainly of basalt. It is roughly equidistant from New Caledonia, New Zealand, and Australia, and its biota generally reflects recent transoceanic dispersal from these three areas. It therefore gives an indication of the ability of the conifer genus *Araucaria*, of which one species is found on the island, to cross large water gaps.

At present one might formulate a general picture of a largely isolated Late Cretaceous-Early Tertiary flora and fauna extending along a broad coastal zone from South America via the Pacific coast of a warmer, more northerly Antarctica to Australia and the New Zealand-Melanesian arc, perhaps with further weak extension towards Asia. The isolation of Australasia was gradually increased by climatic deterioration in Antarctica and decreased in the north by the development of the Indonesian archipelago facilitating waves of invasion by organisms from Asia. The finer detail of this pattern must await intensive geological, oceanographic, and biological surveys of the area.

THE COLLECTION OF DATA

Both the testing of ecological theory and the mapping of distribution patterns are hampered at present by the lack of good data collected specifically for the purpose. If energy is to be devoted to one particular group then the study of the Lepidoptera, especially moths, has much to offer. Moths have several qualities that make them ideal for biogeographical work. They are cosmopolitan with a wide range of dispersive ability; the many species are easily sampled quantitatively with light traps, providing excellent data for statistical analysis; taxonomically they are relatively easy to study, with numerous morphological characters; their distribution patterns show good correlation with those for other dispersive groups of animals; through the specificity of their larval feeding they may reflect to some extent phytogeographical patterns.

During 1971 a colleague and I have been conducting moth surveys in the south-west Pacific, he in Fiji, Tonga, and the New Hebrides, and I in New Caledonia and Norfolk Island. I am optimistic that the results of our surveys will provide the sort of data that will help resolve the problems outlined in this paper.

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ADDENDUM

Since going to press two review articles have been published that are important to the above discussion. Whittaker (1972) has reviewed the literature on the measurement of diversity and discussed its relationship with evolutionary theory. Raven and Axelrod (1972) have related a wide range of plant and animal distribution patterns to an assessment of the geographical history of Australasia from recent literature on plate tectonics.

RAVEN, P. H. and AXELROD, D. I. 1972. Plate tectonics and Australasian paleobiogeography. *Science, N.Y.* **176**, 1579·1386.

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