

A system of world mammal faunal regions

II. The distance decay effect upon inter-regional affinities

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ABSTRACT. Regional/historical biogeography is often considered descriptive and/or highly idiographic by nature. This point of view is challenged here through an analysis in which a newly developed mammal faunal regions classification system is linked to a simple model of evolutionary process. Variations in subregional characteristics are used to examine the view that evolution represents a stochastic spatial process. This is investigated by starting with the proposition that the present spatial arrangement of mammalian faunal elements (families) should be explainable solely on the basis of chance interaction rates among subregions and a deterministic distance decay effect on the diffusion of evolutionary innovations across the system over time. A derivative of the entropy maximization model developed by Alan G. Wilson is employed to separate out the effects of chance interaction among fauna subregions from the second order faunal characteristics used as a surrogate for the distance decay effect. The present distribution of mammal families is shown to be well represented through this model, which accounts for almost all the variance in the original inter-subregional faunal similarities matrix. The normative character of the model and the classification underlying it is further pursued through an examination of within-system characteristics of subregional interrelation. It is shown that, despite variation among subregions with respect to their absolute diversities and other attributes, the characteristics of any individual unit can be used equally well to specify the general properties of the rest of the system, a fact that substantiates the claim that the component units are logically equivalent. It is concluded that a carefully specified system of world faunal regions can be used as a tool through which to infer system level relationships among these interacting units.

Introduction

In part I of this work (Smith, 1983; hereafter referred to as 'part I') a method was introduced through which construction of world faunal regions could logically proceed, together with the results of one such construction. In this work, we shall be concerned with some implications of this classification to the study of faunal regionalization process and

evolution in general. Specifically, it will be shown that this systemization can be used as the basis for a model of regional distribution patterns involving only two interacting factors: (1) the spatially-unconstrained most probable state of interaction among system components; and (2) the influence of a system-wide distance decay effect on the diffusion of evolutionary innovation within it.

The fauna of any given-sized area can be

viewed as having arisen from a complicated historical interplay of a large number of factors. It is usually difficult – or impossible – to collect information on all these factors, and for this reason many might feel that we will never be able to construct a normative model of their sum effects on faunal evolution. But is it actually necessary to have all this information before we attempt to understand evolutionary patterns at the regional level? Idiographic reconstructions of portions of large-scale systems evolving under the influence of a complex of interdependent positive and negative feedback channels may be necessary to view the particulars of general process, but dwelling upon such individual links rarely leads to great insight into system-organizing properties. We may expect great variation of interaction among the subsystem elements of any general system; it is only when we identify and measure the output of the system in total that we are able to put that variation into context.

With regard to the present distribution of organisms (and here we shall be concerned with mammals), the above comments can be put into context by keeping in mind that any given taxon may play spatially varying roles in contributing to the moment-to-moment stability of the world system. This variation over space is to be expected as a natural result of the stochastic temporal process we call evolution. But it also may be viewed as a function of non-biological variations in the frame of reference within which biological evolution unfolds. Regardless of one's view of how evolution occurs at the biological level, at the spatial level it is a process of information diffusion; quite simply, biological innovations succeed at given times and places and spread, through population expansion and/or reference frame alteration (e.g. continental drift), through time and space. Despite the self-evidence of this statement, however, evolutionary process is rarely viewed from this perspective; rather, the tendency has been to use our knowledge of biotic distributions to give more substance to largely aspatial biological process models such as natural selection. It would be more productive, it seems, to put distributional information to use in a way that challenges existing models more directly.

In attempting to move in that direction here, we may begin by making two elemental claims concerning the spatial expression of the evolutionary process. These are that it can be viewed as constrained by: (1) variation in the limits of stochastic change possible within organismal populations; and (2) the continuous but limited surface of the earth. By slightly expanding the first point, we can also reasonably assume that variation must exist among populations with respect to their relative abilities to disperse, become integrated into new community settings, and persist in these new settings. Various means exist through which to study these events independently of one another, but thus taken in isolation (or even in simple sum), they lack the power to deal with the way in which the system recursively develops as a whole. What *can* be said about the system as a whole, combining the claims made above, is that at any given time it will be composed of an immense variety of forms upon which chance events have acted to: (1) bring them into existence at a certain location to begin with; and (2) cause them to have expanded their spheres of influence within their frame of reference to lesser or greater degrees.

This is where the matter would end were it not for the fact that, as soon as a chance innovation has added a new thread to the evolutionary weave, the nature of further change within that thread becomes constrained by deterministic spatial influences. As any biological innovation diffuses away from its point of origin, the influence of its own history becomes more and more of a restriction on its range of possible future paths (both genetic and spatial). Moreover, the characteristics of this distance decay effect vary according to where and when within the system the original innovation took place: direction and rate of diffusion away from a source is strongly influenced by presence of, or lack of, barriers.

This discussion can eventually be led toward a treatment of whether the characteristics of present mammal distribution support the notion that this group has attained a kind of evolutionary equilibrium with regard to its present rates of innovation and extinction. For now, however, we will concern ourselves with a prior and related matter,

examining the causal structure behind present mammal faunal characters and interrelationships. This subject is both intrinsically interesting and directly bears on our earlier discussion of the relative merits of idiographic versus nomothetic investigation in zoogeographic study. We shall begin by looking more closely at some characteristics of the regional classification of part I.

Entropy maximization and entropy minimization in faunal classification

The classification system presented in part I was based primarily on the idea that a regionalization procedure should produce results of maximum efficiency; that is, that the classification arrived at should represent some ideal combination of low redundancy and clear logical delineation. Part of the goal of the analysis was to derive a system of regions any of whose subregions were internally at least as similar to one another as to the subregions of any other region, and yet were within this constraint still as different from one another as possible. This is interesting because it means that the solution obtained is as 'closely packed' as is possible; simply, the subregional units have been defined in such a fashion as to represent a 'minimum entropy' delineation of the results of faunal interaction.

It should not be surprising that we can think of the derivation of biogeographical units as being an exercise in entropy minimization. Systematists since at least the time of Linnaeus have sought to separate logically the diversity of the organic world into carefully delimited and highly structured homogeneous groups of nested 'comparable sets.' Only recently did we obtain a more formal justification for such endeavour: evolution itself can be considered a negentropic process (Schrödinger, 1945); that is, as producing forms of increasing complexity and order. Thus, any classification system designed to represent the products of evolution must itself exhibit a high degree of complexity and order, and especially the second (if it is to be of practical use). The result is that biological systematics – spatial or otherwise – naturally seeks minimum entropy

solutions to the ordering of its subjects of study; in this direction naturally lies a resulting classification of greatest internal logic and least internal redundancy.

Despite the fact that evolution has produced a highly ordered living system, the process itself is usually considered to be stochastic. How this paradox of highly ordered form generated by stochastic events is ultimately to be resolved remains to be seen (see relevant discussions in Schrödinger, 1945; Prigogine, 1947; 1980; Slobodkin, 1962; von Bertalanffy, 1968; and Iberall, 1976), but it seems to me (per earlier comments) that any answer must centrally involve the limits of genetic flexibility as related to, and reflected in, the spatial distribution and diffusion of organisms.

This returns us to the matter of central interest here. I submit (or at least tentatively accept) that the historical record of evolutionary events suggests a stochastic process in which a minimum entropy structural solution has been shaped out of two main constraints, the limits of genetic flexibility and the distance lag associated with innovation diffusion over space. If such is true, and if regional biogeographic patterns can be considered in any fashion indicative of this state of affairs, we should be able to find some supporting evidence for the assertion in those patterns. Otherwise stated, can we obtain evidence from the present distribution of organisms that stochastic processes have operated to produce the non-random patterns of diversity we now witness?

One way to answer this question requires three pieces of information. The first is a minimum entropy classification of the subregional units whose characteristics will be used to explore the matter. This is of no less import in interpreting the products of evolution than is an efficient system of phylogenetic reconstruction, for reasons already stated. The mammal regionalization scheme of part I can be appropriately employed here to this end.

Given the basic units of investigation, it is possible to proceed by erecting the examinable proposition that the present distribution of mammals can be explained as an interaction between two causal forces. These are: (1) an aspatial and random genetic element responsible only for the fact of adapta-

tional variation *per se*; and (2) a spatial and deterministic element constraining rates of interaction across the areal framework of the system. If indeed we discover that the variance inherent in a matrix of inter-sub-regional similarities can be accounted for solely on the basis of these two factors, we might conclude that our minimum entropy regional classification is compatible with a maximum entropy distance decay-based evolutionary model. If we cannot, on the other hand, some fundamental reassessments of our initial premises would seem to be in order.

To put the above notions into an investigational framework, we must separate the variance of the inter-subregional similarities matrix into components representing chance spatial interaction, the distance decay effect, and error. Very little error can be tolerated here, however: we are proceeding under the assumption of an extraordinary well worked-out system (both spatially and temporally), and it is imperative that a very large proportion of the variance be accounted for by the two independent variables (or variable sets) alone. This necessitates rather careful choice of the surrogates to be used for these, and an appropriate model for their interrelation.

Assuming the existence of measurable distance decay effect surrogates (to which matter we shall turn shortly), the relationship between probabilistic outcomes of interaction between system sub-elements and the effect of distance decay/spatial contiguity constraints on such is given by the entropy maximization formulation of Wilson (1970). In this extension of Boltzmann's Law, the most likely state of a multi-element system is given in terms of the following:

$$t_{ij} = A_i O_i B_j D_j e^{-\beta c_{ij}}$$

where t_{ij} is the degree of interaction between locations i and j . In Wilson's work, which concerned estimating rates of interaction between places of residence and places of work, O_i represented number of workers at location i and D_j number of jobs at location j , and c_{ij} the cost of commuting between a given pair of locations. The other elements of the equation (except for the natural logarithm base e) are Lagrangian multipliers that ensure system-wide most probable state constraints are met. Because cost of commuting is directly related

to the distances involved, c_{ij} represents a measure of the distance between locations i and j . For a brief introduction to the Wilson approach, see the excellent discussion by Gould (1972).

Wilson's model has been one of the most important contributions to modern geographical theory. It can be used in the present context to account for the most likely state of faunal similarities among subregions, where similarity is considered as synonymous in meaning to interaction. A multiple regression model can be developed in which similarity is predicted as the combined function of most likely state considerations and an assumed distance decay effect on the diffusion of evolutionary innovation over space. This procedure may be viewed as a generalization of the MacArthur & Wilson (1963, 1967) island biogeography accounting framework. Through their approach, progressive impoverishment of faunas per distance from a given source could be modelled; Wilson's method allows us to interpret the sum of such effects among a number of system elements each of which is simultaneously acting as source and sink. Some problems emerge in operationalizing the model, however: surrogates must be found for the distance decay parameter, and the Lagrangian multipliers must be elicited.

Wilson solves the latter problem by simultaneously calibrating and estimating the multipliers from a given data set via iterative procedures that yield an eventual convergence to stable values. This is impossible here for, although we can use our faunal similarities matrix (Table 3 in part 1) as the basis for estimating a spatially-unconstrained most-probable interaction state configuration, we have no exogenous measure of 'cost' which can be used as a surrogate for the distance decay function.

We can still, however, construct a multiple regression model employing an *implicit* measure of distance decay: the by-subregion characteristics of distribution of the families of each subregion (Table 5 in part I). If we believe that innovation diffusion in the evolutionary sense is regulated by some generalized 'cost' variable dictating change over space as diffusion proceeds (as was suggested earlier), then variations in the relative remoteness and/or contiguities of each subregion should be

manifest in systematic variations in the cosmopolitanism of their faunas. That such variations do in fact exist is evident in Table 5 of part I; the question, however, is whether these have spatial meaning. Without further discussion now, I tentatively accept these indicators as a composite measure of the spatial results of the distance decay effect on the evolutionary development of mammals. Later I will introduce other pieces of evidence supporting this notion.

The use of these measures as a surrogate for the distance decay (cost) factor greatly simplifies matters. In accepting this surrogate, it is no longer necessary to obtain a constrained maximum entropy solution through co-iterative solution of all three multipliers; rather, the elements of the faunal subregions similarities matrix can be directly predicted via regression as a function of: (1) a spatially unconstrained reformulation of the faunal similarities matrix; and (2) the by-subregion distance decay surrogate values. Thus, the effects of distance over time should emerge as a simple direct function of the observed similarities values s_{ij} once the effects of spatially-unconstrained inter-subregional interaction rates have been removed (or vice versa).

A maximum entropy solution to the faunal similarities matrix S can easily be obtained by double standardizing the matrix (see Slater, 1976, for discussion on method and an example of the usefulness of double standardization) so that all rows and columns sum to zero and have a variance of 1.0. (Note that this operation is consistent with our interpretation of each subregional unit within the classification as being logically equivalent: magnitudes of interaction between individual pairs of subregions have no logical meaning unless related to the distributional state of similarities within the system as a whole.) The resulting matrix of values T can be used to estimate via simple least squares regression the original matrix of similarities S . Before we can do so, however, a procedural choice must be made. Do we wish to analyse system-wide characteristics by stringing out as a 100 element vector all s_{ij} and use this as the dependent variable vector predicted by the 100 elements of T , or do we wish to disaggregate S and estimate the elements of each s_j separ-

ately as a function of constraints operating on individual subregions alone? Otherwise stated, should our most probable state be couched in terms relating to a configuration state of interaction based on a 100 by 1 analysis or on ten 10 by 1 analyses? This is an important question, because if we cannot deduce an answer *a priori*, we may be unable to decide later how effective in improving prediction the addition of the distance decay variables are. We must therefore take the time to investigate some differences between the two possible formulations.

Some system characteristics

Weiss (1971: 24–25) has suggested a means of expressing the relationship between a system and its interrelated subsystems: 'The relative constancy of the order of a group as a whole as compared to the much greater variability among the constituent subunits . . . is one of the most crucial criteria, as well as tests, of true system dynamics . . . Considering that any given component, say 'a,' is faced with a wide range of unpredictable fluctuations of its environment, which also includes the other components, 'b, c, d . . . n,' we must assume its reactions to cover a correspondingly wide range; let us designate that range as ' v_a ,' the variance of 'a.' Similarly, the other components, 'b, c, d . . . n,' have each their own range of potential excursions from the mean, i.e. variances ' $v_b, v_c, v_d . . . v_n$.' At the same time, the total system preserves a high degree of *invariability*; that is, despite the seemingly erratic variances of its countless constituents, it does not fly apart. So, we can formulate this experience in an inequality according to which the total variance for the whole system, ' V_s ,' is infinitely less than the sum of the variances, v , for its aggregate components, or $V_s \ll \sum (v_a + v_b + v_c + v_d + . . . v_n)$.'

In essence, what Weiss is expressing in the above is the idea that system invariability (persistence) will usually evolve as a result of interlocking subsystem dependencies. The underlying notion here is that the sum of the interactions among subunits will be deviation-counteracting in a fashion serving efficient operation of the sum unit.

Weiss' comments can easily be related to

the present discussion. The sum of interactions among the faunal units identified in part I may be viewed as deviation-countering in the sense that it represents a greatly ordered system of similarities. (Such order, it will be remembered, is manifest in the packing structure inherent in the intraconfiguration distance matrix associated with the final MDS solution to system-wide between subregions similarities.) Recall, however, that the classification procedure has also had the effect of maximizing the compositional differences among subregions, leaving us with a set of ten 'seemingly erratic variances' to incorporate into our modelling procedure. It is now apparent that our classification permits two very different perspectives on world faunal structure: one in which variation in the magnitudes of interaction between faunal units is emphasized to produce a view of the diversity within the system (regional differences), and another in which the equal logical standing and interrelatedness of units is focussed on to produce a view of system order and unity. The perspective we decide to take under given conditions will determine the appropriate route of analysis.

Given the fact of differing-sized regional faunas, we should therefore expect to come up with somewhat differing results in simultaneously regressing all 100 similarity values with the doubly standardized values than in performing regressions involving each subregional similarities vector individually. The residuals from each operation are plotted against the dependent variable on a subregion by subregion basis in Fig. 1. Residual values are identified and tabulated in Table 1; information on the regressions themselves is presented in Table 2. Considerable differences do in fact surface. Residual series from the 'world system' regression, plotted on a subregional basis, exhibit varying degrees of positive or negative correlation with the dependent variable. Moreover, when disaggregated in this fashion, they do not individually sum to zero. The first condition is indicative of an incomplete regression model. Given the form of the residual series and the apparent relationship between residual magnitude and degree of contiguity between associated subregions (as interpreted via Table 1), it is tempting to think that we are lacking an explanatory

variable accounting for a spatial constraint factor. The sign of the correlation in each series can be construed as indicating whether the mammal fauna of a particular subregion figures more or less prominently than average in the make-up of the faunas of the rest of the subregions. The fact that each subregional residual series does not sum to zero results from the disaggregation operation, and ultimately from the differences in simple mean magnitudes of values in each vector of similarities (see the marginal statistics of Table 3 in part I).

The residual plots in Fig. 1 associated with the ten subregional regressions provide a different perspective on system interaction. There, each residual series sums to zero; this is to be expected as each plot identifies the *relative* importance of each subregion's fauna on any particular subregional fauna once absolute magnitude of interaction effects have been removed. The result is for each subregional plot a 'peaked' distribution of values again inviting a distance decay effect interpretation, since residual magnitude (absolute value) is correlated with similarity.

As can be viewed in Table 2, the regressions are highly significant; it is quite apparent that the greater part of mammal distribution on the earth's surface can be accounted for on a contiguity-unrelated most-probable-state configuration basis alone. This should not discourage us, however, as the residual plots of Fig. 1 still indicate an incomplete model. Regardless, we have yet to answer the question of which residual series it is that we wish to predict from our two variable measures of the distance decay effect. We can now proceed to this matter.

Although the sum estimation of within-system relationships may necessitate a multi-dimensional solution, distance itself is a scalar whose relative magnitude with respect to other distances can be expressed in one-dimensional terms. This is as true in specifically biological models such as that of MacArthur & Wilson (1963, 1967) as it is in the Wilson (1970) formulation discussed earlier. This information allows us to choose between the two types of residual series under consideration. From the world system regression plots in Fig. 1 it is evident that very different functions of variable correlation are involved from

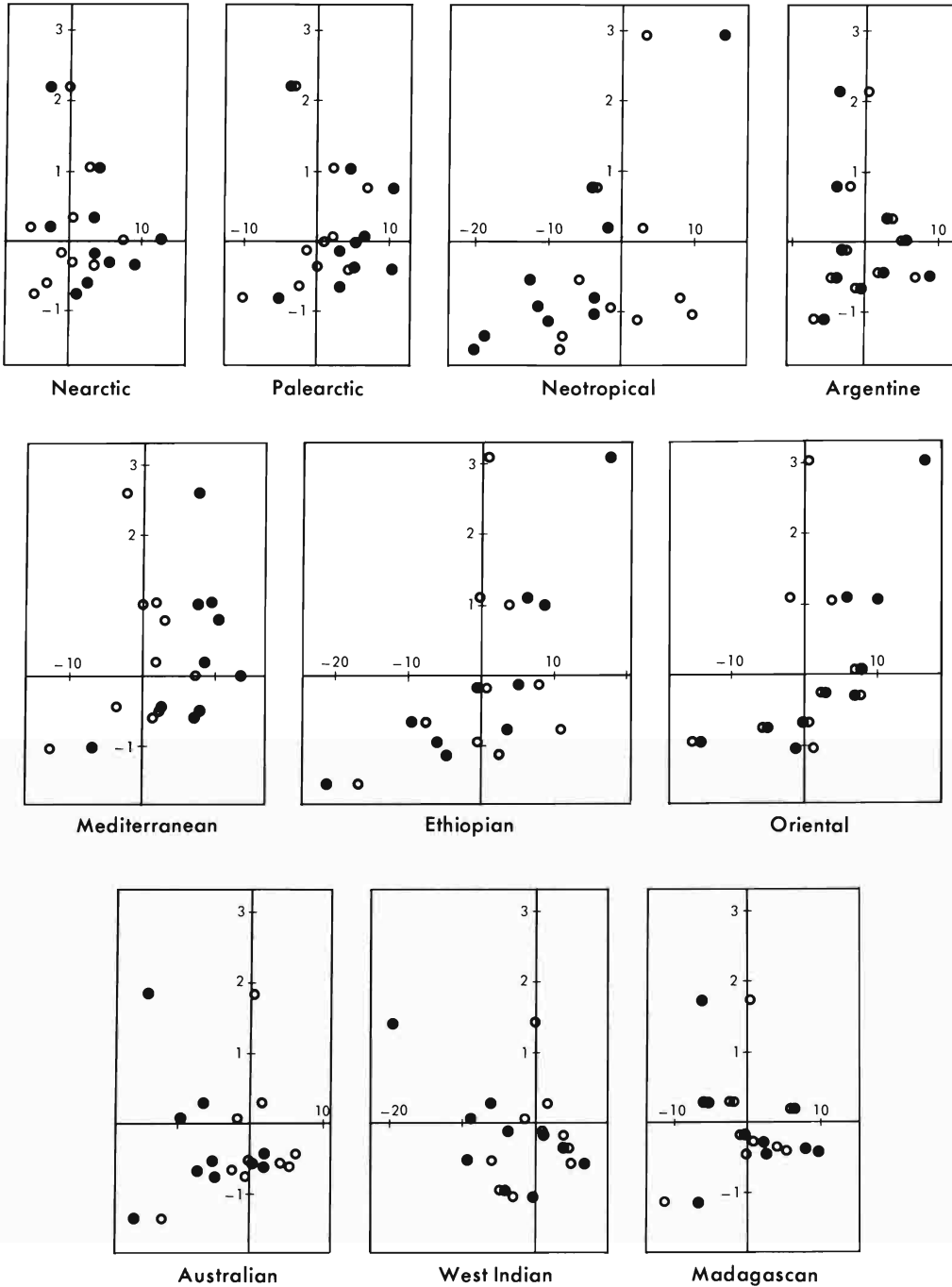


FIG. 1. Plots of values of residual vectors p_j (open circles) and r_j (filled circles) against corresponding values of vectors s_j from Table 3 in part I. Ordinate values (s_{ij}) have been standardized. All values are dimensionless. See text for explanation.

TABLE 1. Matrices P and R of residual values disaggregated on a subregional basis and plotted in Fig. 1. Elements of P are from the individual subregional regressions; elements of R are from the world system regression.

	Nearctic	Palaearctic	Neotropical	Argentine	Mediterranean	Ethiopian	Oriental	Australian	West Indian	Madagascan
Matrix P										
Nearctic	-0.1	2.3	3.1	3.6	7.4	11.1	7.8	4.2	3.8	4.1
Palaearctic	3.0	-3.1	8.2	5.2	3.0	7.9	6.9	5.5	4.6	5.3
Neotropical	-5.5	-10.3	3.5	-2.1	-12.7	-17.3	-15.7	-12.3	-6.0	-11.4
Argentine	0.4	0.9	-3.4	0.5	2.4	2.4	0.7	-0.2	0.8	-0.2
Mediterranean	7.6	7.1	9.9	7.0	-2.2	3.7	3.8	6.3	4.9	6.2
Ethiopian	-4.8	-1.3	-8.5	-7.1	0.1	0.7	-1.9	-2.6	-5.0	-0.8
Oriental	0.4	2.1	-1.3	-1.4	2.0	-0.3	0.7	-0.8	-3.2	0.6
Australian	-3.2	-2.4	-8.0	-4.7	-3.5	-7.9	-5.9	0.4	-1.6	-2.4
West Indian	-1.1	0.1	-5.8	-2.8	1.7	-0.8	1.3	-1.9	-0.2	-1.7
Madagascan	3.3	4.6	2.3	1.8	1.9	0.4	2.2	1.5	2.0	0.4
Matrix R										
Nearctic	-2.8	4.9	-2.0	3.2	13.6	3.7	7.3	0.3	1.0	8.0
Palaearctic	4.3	-3.3	-3.9	5.6	10.5	5.1	8.2	1.9	4.0	10.0
Neotropical	-2.7	-5.0	14.0	-3.9	-6.7	-21.7	-14.3	-16.2	-9.6	-6.9
Argentine	3.6	5.5	-3.4	-3.7	8.2	-4.8	-0.0	-5.2	-3.8	2.8
Mediterranean	12.9	10.7	-3.9	8.4	8.0	8.7	10.2	2.2	6.7	6.3
Ethiopian	1.1	3.4	-20.4	-5.7	8.0	18.7	5.9	-7.5	-4.1	-0.3
Oriental	5.7	6.8	-11.7	-0.3	9.9	6.2	16.7	-4.9	-0.6	2.4
Australian	2.4	3.3	-18.9	-4.3	2.7	-9.8	-5.7	-14.3	-9.0	-6.3
West Indian	3.5	5.5	-12.7	-2.9	7.4	-6.1	-1.2	-9.7	-20.4	-5.3
Madagascan	9.1	10.5	-10.0	2.7	8.7	-0.7	3.0	-6.5	-6.1	-14.5

TABLE 2. Results of the least squares regressions producing residual values listed in Table 1. See text for explanation.

	Nearctic	Palaearctic	Neotropical	Argentine	Mediterranean	Ethiopian	Oriental	Australian	West Indian	Madagascan	World system
Dept variable	($s_j=1$)	($s_j=2$)	($s_j=3$)	($s_j=4$)	($s_j=5$)	($s_j=6$)	($s_j=7$)	($s_j=8$)	($s_j=9$)	($s_j=10$)	(S)
<i>N</i>	10	10	10	10	10	10	10	10	10	10	100
Indpt variable	$v_j=1$	$v_j=2$	$v_j=3$	$v_j=4$	$v_j=5$	$v_j=6$	$v_j=7$	$v_j=8$	$v_j=9$	$v_j=10$	<i>V</i>
F value	180.9	138.8	164.6	159.4	148.8	110.4	129.1	94.5	117.3	80.2	588.7
Signif	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
<i>r</i> ²	0.958	0.946	0.954	0.952	0.947	0.932	0.942	0.922	0.936	0.909	0.857

subregion to subregion; we would assume (if these patterns are taken to be indicative of a significant distance decay effect) that these differing functions taken in simple sum would lead to a complex world system distance decay function (that is, a multidimensional function arising from an initial choice to treat all subregional units as functional inequivalents). This is true whether the sign of the residuals is retained or not. The subregion regressions, however, yield more or less uniform residual plot patterns which seem conducive to a one-dimensional system-level distance decay interpretation (because our initial choice here has been to focus on the functional equivalence of each individual subunit's standardized contribution to total system order). But can this be verified? That is, can we confirm a one-dimensional interpretation of the latter residual series and in so doing obtain a simple system-wide distance decay coefficient? Luckily, this question can be answered directly and unambiguously.

Our general test proposition is that the state of interaction (similarity) s_{ij} should be predictable virtually entirely on the basis of most-probable-state and distance decay function indicators alone. Given the removal of that portion of the system variance associated with spatially-unconstrained most-probable-configuration of interaction, that variance left unexplained should be due largely to the effect of distance decay. Therefore, the matrix of residuals *P* left should be in some sense one-dimensional, whereas the matrix of residuals *R* left should require higher-dimensional interpretations. This can be ascertained by translating each matrix into a similarities matrix, applying MDS, and examining for each analysis the stress values associated with different dimensional solutions.

The elements of the matrices tested can be derived by summing the differences in residual values of each subregional pairing common to each regression, or:

$$o_{ij} = \sum_{k=1}^{10} |z_{ik} - z_{jk}|$$

The scaled solutions to the world system version exhibit a stress of 0.056 for two dimensions and 0.144 for one dimension. The subregions version equivalents are 0.007 and 0.048, respectively. The last value signifies a

TABLE 3. Results of the stepwise least squares regressions employing column vectors s_j as the dependent variables and vectors p_j , f_1 and f_2 as the independent variables. See text for discussion.

	Nearctic	Palaearctic	Neotropical	Argentine	Mediterranean	Ethiopian	Oriental	Australian	West Indian	Madagascan
Dependent variable	($s_{j=1}$)	($s_{j=2}$)	($s_{j=3}$)	($s_{j=4}$)	($s_{j=5}$)	($s_{j=6}$)	($s_{j=7}$)	($s_{j=8}$)	($s_{j=9}$)	($s_{j=10}$)
Independent variable 1	$v_{j=1}$	$v_{j=2}$	$v_{j=3}$	$v_{j=4}$	$v_{j=5}$	$v_{j=6}$	$v_{j=7}$	$v_{j=8}$	$v_{j=9}$	$v_{j=10}$
F value	582.4	185.1	360.2	522.1	123.6	292.4	457.0	539.5	20.4	187.3
(sig.)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.004	0.000
Independent variable 2	f_1	f_1	f_1	f_1	f_1	f_1	f_1	f_1	f_1	f_1
F value	25.9	27.5	8.6	16.6	9.4	19.6	37.7	53.0	23.5	19.1
(sig.)	0.002	0.002	0.026	0.007	0.022	0.004	0.001	0.000	0.003	0.005
Independent variable 3	f_2	f_2	f_2	f_2	f_2	f_2	f_2	f_2	f_2	f_2
F value	5.5	6.3	9.1	6.7	0.4	1.4	0.4	16.4	0.0	3.0
(sig.)	0.057	0.046	0.023	0.041	0.540	0.286	0.554	0.007	0.850	0.135
Overall F	260.5	203.1	143.0	176.6	101.2	127.9	248.6	257.7	153.7	98.7
(sig.)	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Overall R^2	0.992	0.990	0.986	0.989	0.981	0.985	0.992	0.992	0.987	0.980

good one-dimensional fit, and confirms our expectations that use of the residuals p_{ij} from the individual regressions is the more appropriate route in the testing of our general hypothesis.

Interaction vectors s_j can now be regressed with the most-probable-configuration state vectors t_j and the two distance decay surrogate vectors (f_1 and f_2). The results are given in Table 3. Obviously, the model is a very good one; all multiple r s are above 0.99 and the combined distance decay measure in each case adds significantly to the regression model. With such a high proportion of the variances explained, credence is given to the idea that the distribution of world mammal faunas is a function of: (1) its spatially-unconstrained most-probable-interaction state configuration; and (2) a system-balanced distance decay factor associated with the stored effects of lag over space and time on the diffusion of evolutionary innovation.

Some characteristics of within-system order

It remains to be shown in a technical sense how well the system specifies itself internally. This is of interest in promoting a better understanding of how the subregions of the system are related to one another, and is necessary to confirm the functional equivalence of the subunits of the classification with respect to each's implicit information content. Four sets of relationships are briefly discussed here: (1) prediction of subregional faunal characteristics (vectors f_1 and f_2) from subregional similarities statistics (vectors m_1 and m_2); (2) prediction of subregional diversities (vector $s_{i=j}$) from subregional faunal characteristics (f_1 and f_2); (3) prediction of subregional faunal characteristics (f_1 and f_2) from degree of subregional importance with respect to other subregions; and (4) prediction of subregional diversities ($s_{i=j}$) from degree of subregional importance with respect to other subregions. The results of the least squares regressions associated with these four sets of analyses are presented in Table 4; short descriptions of each analysis follow. These and other system characteristics will be considered in greater depth at a future date.

(1) The purpose of this analysis was to determine how well the unique characteristics of the mammal fauna of each subregion could be predicted from the vectors of marginal statistics (m_1 and m_2) of the similarities matrix of Table 3 in part I. Put in other terms, I wanted to determine how well the characteristics of cosmopolitanism of each subregional mammal fauna could be specified by system properties summarized at the subregional level. To accomplish this, it was convenient to reduce the elements of f_1 and f_2 to a single dependent variable (f_3), their associated coefficients of variation (each of which may be referred to as a subregional 'relative dispersion' value). As can be viewed in Table 4, the results are quite satisfying from the perspective of a system of internal logical order: the dependent variable is well specified by the combination of vectors of means and standard deviations alone. Thus, the system has diversified over time and space in such a fashion that the vector of relative dispersions has become synonymous with the characteristics of within-system diversity of degree of interrelatedness.

(2) Here, the total familial diversity of each subregion ($s_{i=j}$) is predicted as a function of f_1 and f_2 . The results indicate the absolute diversity of each subregion to be strongly related to the characteristics of cosmopolitanism of each subregion a not unexpected result.

(3) These ten regressions give a picture of how the vector of relative dispersion values (f_3) is related to distance decay effects within the system. The independent variables for each regression are derived in the same general fashion as the values o_{ij} for the similarities matrix used to test residual dimensionality via MDS earlier, but with one difference. Instead of removing all signs and treating the values as magnitudes (distances), the signs are retained, allowing a separation into two series for each subregion, one positive and one negative. For example, in considering the relationship between the Nearctic and Palearctic subregions with respect to both direct and indirect effects of distance decay, there are ten such values to tally: one each for Nearctic-Palearctic residual comparison in each subregional regression. The sum of the negative residuals represents case one of column x_1 of a new ten element by ten element matrix X ;

TABLE 4. Results of the least squares regressions associated with four within system analyses. See text for explanation.

Analysis 1:	Dept var.	Indpt var. 1	F value (sig.)	Indpt var. 2	F value (sig.)	Overall F (sig.)	Overall R^2			
	f_3	(column means, Table 3, pt 1)	454.9 (0.000)	(col. pop. st. devs., Table 3, pt 1)	530.9 (0.000)	417.4 (0.000)	0.992			
Analysis 2:	Dept Var.	Indpt var. 1	F value (sig.)	Indpt var. 2	F value (sig.)	Overall F (sig.)	Overall R^2			
	$s_{i=j}$	f_1	11.6 (0.001)	f_2	79.5 (0.000)	52.8 (0.000)	0.938			
Analysis 3:										
	Nearctic	Palaearctic	Neotropical	Argentine	Mediterranean	Ethiopian	Oriental	Australian	West Indian	Madagascar
Dependent variable	f_3	f_3	f_3	f_3	f_3	f_3	f_3	f_3	f_3	f_3
Independent variable 1	$x_{j=1}$	$x_{j=2}$	$x_{j=3}$	$x_{j=4}$	$x_{j=5}$	$x_{j=6}$	$x_{j=7}$	$x_{j=8}$	$x_{j=9}$	$x_{j=10}$
F value (sig.)	7.2 0.032	2.6 0.154	99.4 0.000	30.9 0.001	9.4 0.018	36.7 0.001	22.4 0.002	136.4 0.000	92.5 0.000	24.0 0.002
Independent variable 2	$y_{j=1}$	$y_{j=2}$	$y_{j=3}$	$y_{j=4}$	$y_{j=5}$	$y_{j=6}$	$y_{j=7}$	$y_{j=8}$	$y_{j=9}$	$y_{j=10}$
F value (sig.)	54.2 0.000	67.9 0.000	16.1 0.005	16.3 0.005	112.5 0.000	29.9 0.001	53.4 0.000	0.8 0.388	8.5 0.023	26.9 0.001
Overall F value (sig.)	39.3 0.000	37.9 0.000	52.2 0.000	48.5 0.000	56.2 0.000	45.7 0.000	49.9 0.000	80.7 0.000	65.3 0.000	39.0 0.000
Overall R^2	0.918	0.915	0.937	0.933	0.941	0.929	0.934	0.958	0.949	0.918
Analysis 4:	Dept var.	Indpt var.	F value	Signif.	r^2					
	$s_{i=j}$	(means of $q_{i=1,10}$)	237.6	0.000	0.967					

the sum of the positives, case 1 of column y_1 of a new matrix Y . To recount, we begin by identifying the values $p_{1,1} - p_{1,2}$, $p_{2,1} - p_{2,2}$. . . $p_{10,1} - p_{10,2}$, partitioning the results into negative and positive values, and summing these individually to arrive at the elements $x_{1,2}$ and $y_{1,2}$ of two new matrices. Once all these values have been derived, the elements of the relative dispersions vector (f_3) are then

regressed with the elements of subregional column vectors x_j and y_j .

It may not seem worthwhile to go to all this trouble, but the results are quite illuminating. What can be viewed is the way over-representation of subregional faunas in other subregional faunas is in a sense compensated for by under-representations elsewhere. For the entire system to be truly self-specifying, a

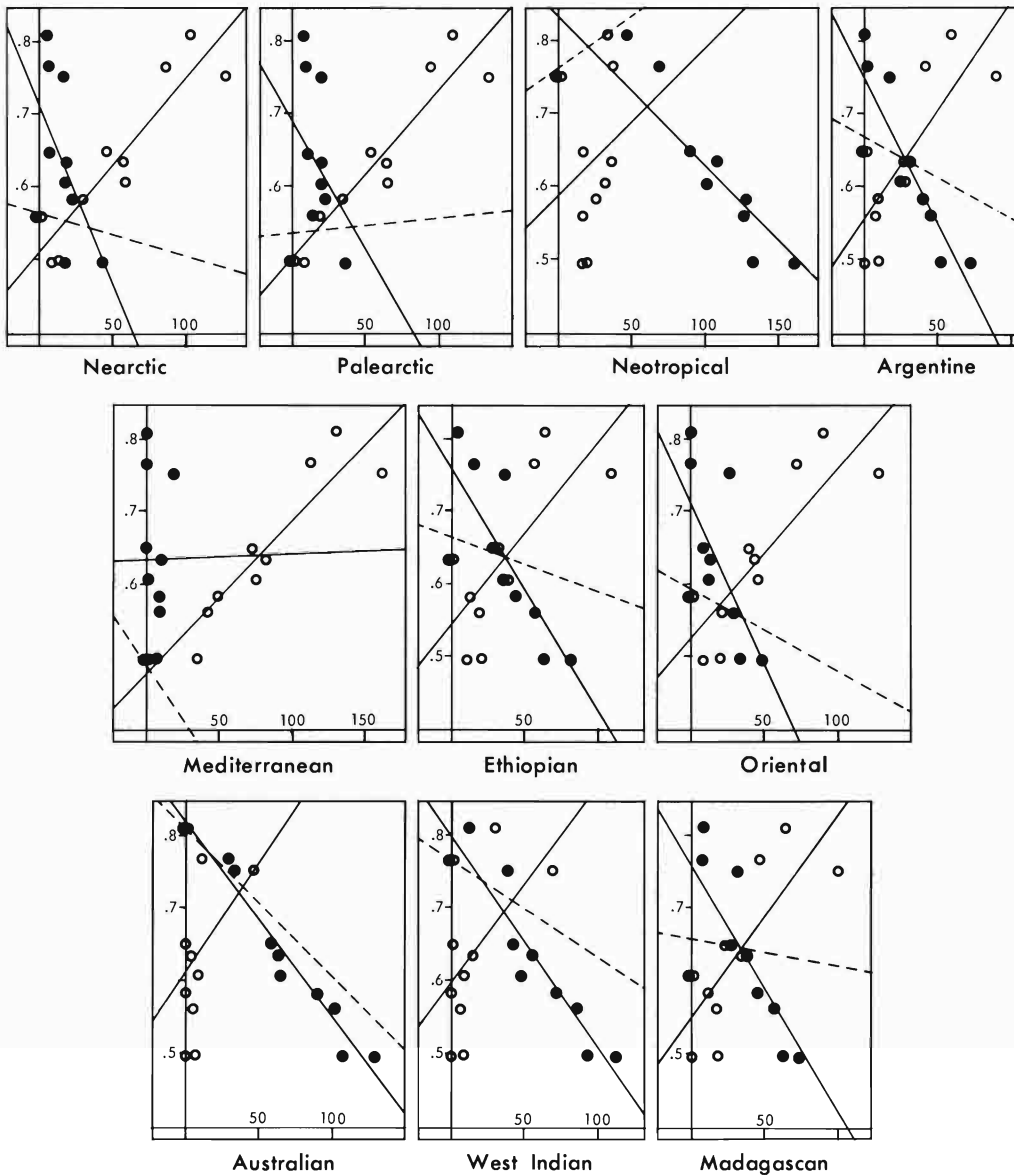


FIG. 2. Plots of values of vectors x_j (filled circles) and y_j (open circles) against corresponding values of vector f_3 . All values are dimensionless. See text for explanation.

balance must obtain that at once accounts for chance and differences among subregions with respect to area and mean spatial location within the system, and their varying faunal diversities. The multiple regressions again indicate a high degree of predictiveness, and for all subregions. More instructive than these results, however, are the scattergrams of x_j and y_j plotted against f_3 in Fig. 2.

It will be noted that the slopes of all x_j and y_j are quite consistent in Fig. 2 (with the one exception of x_5 , which is hardly correlated with f_3). This pattern illustrates the system-wide solution to distance-induced lag among the diffusing faunas of its sub-components. Also note that the multiple regression estimator line representing those situations in which predictor values are equal (the dashed line in each plot in Fig. 2) passes through $x = 0$ in all ten plots quite near to the plotted $x_{i=j}$ and $y_{i=j}$ values. These are, in effect, the solution values representing what the nature of the fauna should be in each given situation of contiguity relationships and area. It would thus appear that the characteristics of each subregion's mammal fauna cannot be reasonably understood without recourse to study of the system in sum. This is indicated all the more when we discover that: (1) the marginal statistics vectors m_1 and m_2 derived from the original similarities matrix S are entirely uncorrelated; and (2) that the vectors of estimated values associated with the slopes of x_j and y_j in Fig. 2 are also uncorrelated. There is no relationship between mean similarity of subregions to other subregions and variation in such similarity, a fact that also supports the interpretation of evolution as a stochastic process that operates over space as well as over time.

(4) On the basis of the preceding, it is not surprising to discover that the absolute diversity of each subregion can be well predicted by the means of the associated row vectors ($p_i - r_i$) = q_i . The matrix Q is given in Table 5, together with its row and column sums. A graphic representation of these values may be gained by looking at the directional distance between paired plotted points in each scattergram in Fig. 2. Q summarizes the strain on the system devolving from the interplay of most-probable-state configuration and distance decay constraints. Column vectors q_j com-

TABLE 5. Matrix (Q) of values derived by subtracting the elements of P from those of R . See text for explanation.

	Nearctic	Palaearctic	Neotropical	Argentine	Mediterranean	Ethiopian	Oriental	Australian	West Indian	Madagascan	Row sums
Nearctic	-2.7	2.7	-5.1	-0.4	6.2	-7.5	-0.5	-3.9	-2.8	3.9	-10.2
Palaearctic	1.3	-0.2	-12.0	0.3	7.5	-2.9	1.3	-3.5	-0.6	4.7	-4.2
Neotropical	2.8	5.3	10.6	-1.8	6.0	-4.4	1.4	-3.9	-3.6	4.5	17.0
Argentine	3.2	4.7	-0.1	-4.1	5.8	-7.3	-0.7	-5.0	-4.5	3.0	-4.9
Mediterranean	5.3	3.7	-13.8	1.4	10.2	4.9	6.4	-4.1	1.8	0.1	15.9
Ethiopian	5.9	4.7	-11.9	1.4	8.0	18.0	7.8	-4.9	0.9	0.5	30.5
Oriental	5.3	4.7	-10.4	1.1	7.9	6.6	16.1	-4.1	2.6	1.8	31.4
Australian	5.6	5.7	-11.0	0.5	6.2	-1.8	0.2	-14.7	-7.4	-3.9	-20.6
West Indian	4.6	5.3	-6.9	-0.1	5.7	-5.4	-2.5	-7.7	-20.2	-3.6	-30.7
Madagascan	5.8	5.8	-12.3	0.9	6.8	-1.1	0.8	-8.0	-8.1	-14.9	-24.4
Column sums	37.2	42.2	-72.8	-0.8	70.2	-0.8	30.2	-59.8	-41.8	-3.8	0.0

prise elements representing relative rates of presence of that subregion's mammal fauna in the mammal faunas of other subregions. Row vectors q_i consist of elements representing relative rates of presence of other subregions' mammal faunas in its own. q_1 and q_2 are themselves slightly correlated ($r = 0.303$), as would be expected (since the distance decay factor is still implicit in the residuals leading to their construction).

Concluding remarks

While the work reported here began as an exercise in classification, the ensuing analysis may be viewed as having greater general relevance. A cursory examination of it might lead to the impression that it represents yet another effort to overrate the importance of faunal association measures in providing information about inter-regional relationships. This is not the case, however. In point of fact, the actual degree of resemblance between any two particular subregional entities is of little importance in the present work except in so far as this can be compared to the sum of all resemblances across the system. With all faunal units in the classification derived as functional equivalents, the goal of analysis changes. No longer can the criticism be levelled that we are lacking the information on evolutionary rates needed to proceed to comparative study; such information is inherent in the form of the distance decay function itself, a spatial rate referable to evolution at the regional biogeographic level. The distance decay function provides a basis for understanding the pattern of present distributions as the end result of a system of implied flows. We can next proceed in unbiased fashion to a consideration of the factors underlying these, since no assumptions about their nature (for example, the possible contributing specifying effects of dispersal, vicariance events, past and present geographical linkages, ecological constraints, etc.) have been made prior to their identification.

The rationale for this approach can perhaps be understood more clearly by referring back to the original applications of the Wilson entropy maximization model to the study of traffic flows. It can hardly be denied that the

contiguity effects identified in related investigations exist; of more far-ranging interest to regional planners, however, is the spatial basis of these as related to the actors upon the stage. The monetary cost of travel represents an imperfect departure point upon which to base an understanding of distance decay effects upon the spatial distribution of commuting rates: other influences such as the perceived value of time lost to commuting also come into play in their specification. Similarly, in the biogeographic situation present Euclidean distances among regional units prove to be very incomplete indicators of the distance decay effects among faunas. I have shown here, however, that subregion-specific faunal cosmopolitanism statistics provide an extremely good measure of the distance decay effect. What I have not shown, nor attempted to show, is specifically how to dissect these measures into their component influences, historical and ecological (though I believe this can be accomplished).

In closing, brief commentary should be made on the relation of the present study to the fundamental difference between regional biogeographic analysis and vicariance approaches. The latter, idiographic in spatial context and dependent on a largely preconceived notion of the way evolution proceeds, can provide us with little understanding of how evolution unfolds as a spatial/temporal phenomenon. The study of the regionalization process *per se* demands answers to different questions than are asked in the study of how the results of natural selection are distributed over space and time, an area of investigation to which vicariance analysis methods are well suited. Wallace, as much geographer as biologist, had little difficulty in discerning the fundamental dichotomy of approach involved here (between 'zoological geography' and 'geographical zoology'); would that this early understanding had been better developed than in fact has taken place. Regional biogeographic studies have thus been degraded to the status of 'contributory information' subservient to a process, evolution, whose temporal unfolding (phylogenesis) is conveniently supposed to occur 'in space' but not as a part of spatial evolution. This point of view, when compared to twentieth century developments in the theory

of space and time in such fields as philosophy, physics, geography and psychology, is philosophically so archaic as to be embarrassing, and diehard defences of the priority of idiographic methodologies in biogeographic studies can only serve to aggravate this condition.

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