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Experimental Biogeography: Interactions between Stochastic, Historical, and Ecological Processes in a Model Archipelago

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If it had not been so hot on 20 July 1944 in Rastenburg, Germany, the geopolitical face of postwar Europe might have been completely different. Because of the heat, Adolf Hitler moved his daily conference from the underground bunker in which he normally received briefings to a wooden hut. When the bomb hidden in Colonel Stauffenberg's briefcase exploded, the force dissipated much more readily than it would have in the underground bunker; Hitler escaped. If the assassination attempt had been successful, World War II probably would have ended earlier and with a profoundly different peace settlement. Hitler was unsure whether to attribute his survival to chance, calling it "incredible luck," or to determinism, saying, "More proof that Fate has selected me for my mission" (Toland 1976, 799–800).

The Second World War will never be refought, and we will never know what might have happened had 20 July been a cold day. Similarly, biogeographical history cannot be replayed, leaving biogeographers with a dilemma: are today's biogeographical patterns the product of essentially deterministic processes, or are they contingent on a series of stochastic events? For example, how many species of *Anolis* would evolve if the last ten million years were played over again? What if the relative timings of eustatic and geological events in the Caribbean had been different? How would their distributions differ had *Anolis* populations been more extinction-prone or less constrained by interspecific competition? Colwell and Winkler (1984) attempted to address these problems: "If we could seed a series of virgin, replicate earths with primordial life and then set the level of interspecific competition differently in each, could we tell them apart three billion years later by looking at biogeographical patterns?" (p. 344). The processes of replication and repeatability, usually fundamental to the testing of scientific hypotheses, are not available to biogeographers. They must instead rely on comparative studies in order to arrive at general theories of diversity.

Most modern-day communities have developed side by side with changes in their physical environments, interacting with them in a necessarily stochastic manner. After millions of years, over which regional biotas are exposed to a unique sequence of physical changes, over which historical events build on one another, and during which reaction to the changing physical environment is a probabilistic process, one is left with a sample size of one community. In order to increase the sample size, it is necessary to incorporate communities that differ ecologically, historically, or both.

It is therefore pertinent to ask: To what extent are the relevant properties of biotas susceptible to these structuring influences? How resistant are various biotas to the vagaries of stochastic interactions? To what extent are biotas shaped by particular regional geographical history? Are there methods for ascertaining the influence of such processes? Every instance of faunal buildup generates only one result; therefore the nature of the distribution of all possible outcomes must be established before the result can be usefully compared with others. The species diversification process may feed back on itself positively (generating a large variance in the final species count), negatively (generating a smaller variance), or the process may be "memoryless" (of intermediate variance). By understanding the answers to these questions in an artificial setting, conclusions from comparative studies may be interpreted more meaningfully.

Given the differences in the life history strategies and dispersal abilities of different taxonomic groups, it seems likely that ecology, chance, and history will play different roles in shaping their respective biogeographies. Elucidation of the factors determining biogeographical distributions would be aided by knowledge of the influence chance, history, and ecology have on different types of organisms. Field biologists should be aware a priori of the possible biases in the influence of these three structuring forces, and take them into account when attempting to establish generalizations from comparative studies. Information of this nature is a prerequisite for the study of community patterns such as the species-area relationship, patterns of endemism, and niche packing.

Motivated by the challenges outlined by Ricklefs (1987) and inspired to "play God" by the work of Colwell and Winkler (1984), we propose to experiment with biogeography, exploiting the computer to model faunal buildup over ecological and evolutionary time scales in an omniscient fashion. We create and examined a model system in which vicariant events, phyletics, and ecology are all perfectly known; we exploit this hypothetical "archipelago" to explore interactions between ecological and historical processes and to determine their influence on local and regional diversity. In our model, geological history is an independent variable overseeing the interaction of ecologically prescribed taxa with chance events. Mechanisms are developed that allow the evolution of faunal buildup to be replayed repeatably over a fixed geological history. This enterprise allows us to overcome the problems of unit sample size and to investigate the variability inherent in historical and ecological processes. In so doing, we are forced to adopt a broader perspective than commonly required in empirical studies and to formulate a synthesis from a wide spectrum of disparate processes operating on different scales. This process has generated some observations and questions for which we have no satisfactory explanations. Since our approach remains embryonic, we have been tempted into conjectures that, if not entirely justified, we hope will at least be provocative.

DESCRIPTION AND JUSTIFICATION OF OUR APPROACH

The Model

The functions and parameters used for our simulations are laid out in table 11.1. The model simulates the fragmentation of one large island of area (A_S) over an arbitrary number of "vicariant" time units (V_T). The probability of island i splitting in any one "vicariant" time unit is a decreasing function, $V(a_i)$, of island area a_i. Total area is conserved throughout the simulation, with the size of a "daughter" island determined as a randomly selected fraction of the "mother" island. Upon splitting, the two new islands are allotted randomly selected speeds and directions, which are maintained until the occurrence of a subsequent split. It is thus possible to model the development of a random archipelago with a completely known geological history.

Table 11.1 Functions and Parameters Used in the Simulations

$V_T = 100$

$A_S = 100$

$V(a_i) = 0.2a_i/A_S$ if $a_i > 5$; 0 if $a_i < 5$

$D(d_{i,j}) = e^{-kd_{ij}}$

$k = 10, 1, 0.75, 0.5, 0.1$

Extent to which species i with niche coordinates (x_i,y_i) would potentially compete for resources (x,y):

$C(i,x,y) = e^{-2q\sqrt{(x_i - x)^2 + (y_i - y)^2}}$

$q = 1, 0.75, 0.5$

$N(a_i) = 20\, a_i / (50 + a_i)$ Niche radius $= \sqrt{N(a_i)/3.14}$

Probability of species i with niche coordinates (x_i,y_i) becoming extinct on island j with n species present in one 'ecological' time unit:

$E(a_i,s_{ij}) = e^{\,ca_i}(1 + s_{ij})$

$c = 5, 0.9, 0.5$

where $s_{ij} = \sum_{r=1\, r<>i}^{n} e^{-2q\sqrt{(x_r - x_i)^2 + (y_r - y_i)^2}}$

$T_c = 0.367$

$E_T = 20$

$T_s = 0.1$

$T_{ex} = 0.54$

The simulation models the evolution of a radiation within an intermediate-ordered taxon. The original island is seeded with one species representative of the taxon being modeled. Properties of taxa that are considered to remain constant within a radiation are vagility, propensity for interspecific competition, and proneness to extinction.

Vagility is modeled using a function, $D(d_{i,j})$, that yields the probability of dispersal between islands i and j, separated by a distance $d_{i,j}$. Vagility is increased by decreasing the taxon-specific constant k.

Each species has coordinates describing its *mean* position in a two-dimensional niche space that correspond to the species' use of two hypothetical resource distributions. The original seed species is assigned to the point (0,0). Associated with the mean niche position is a function, $C(i, x, y)$, describing in what region of niche space species i (with niche coordinates x_i,y_i) would *potentially compete* for resources x,y in the vicinity of its mean niche position. Increasing q effectively broadens the niche and increases the proportion of resources sequestered by a species on any one island. This function permits an estimate of the level of interspecific competition experienced by a population of a species on a particular island. The function $N(a_i)$ relates the available niche space on island i to its area a_i; niche space available on smaller islands are nested subsets of larger ones. The mean niche position of a species randomly "walks" within the available niche space at a random pace, unless it wanders into an area of niche space for which interspecific competition for resources is above a certain threshold (T_C). In this case the niche position moves in the direction that minimizes competition at a pace proportional to the level of competition encountered.

An extinction function, $E(a_i, s_{ij})$, defines the probability that a population of species j on island i will go extinct, where s_{ij} is the level of interspecific competition species j is experiencing on island i. The exponent c allows us to alter the "proneness" to extinction of the taxa involved in any particular run.

Every vicariant time unit is subdivided into an arbitrary number of "ecological" time units (E_T) in which each population of extant species on every island has a probability of: (1) dispersing from the islands on which they are found to all other islands; (2) becoming extinct; and (3) niche position evolution. When a population of a particular species becomes sufficiently isolated (i.e., the probability of immigration from other conspecific populations falls below a specified minimum T_S), the population is considered to undergo speciation. A species can only successfully disperse to an island if its required resources (as defined by its niche coordinates) are present on that island (as defined by $N(a_i)$) and if the level of competition for those resources is below a specified threshold T_{ex}.

Unless two islands have identical species compositions, conspecific populations of a species on different islands will be exposed to different *local* interspecific conditions. The change in the species niche position is therefore the average of the forces acting on the niche position on each island population. When an island breaks up, it obviously becomes smaller, and the available niche space, defined by $N(a_i)$, declines. The biota on the two new islands are replicates of the original biota on the island before vicariance, except for those species whose required resources fell within the lost niche space (and therefore go locally extinct). Probabilistic events are deemed to have occurred if a random number (0–1) is selected less than the probability of the event occurring. Uniformly distributed random numbers are generated from a function utilizing a predefined seed.

Assumptions

No attempt was made to estimate parameter values from empirical data; the model was developed entirely abstractly. The time scale is assumed large enough to allow at most two thousand sequential speciation events in any one lineage. In any simulation attempting to integrate an ecological with a geological time scale, it is necessary to view ecological time in a very coarse grain. It should be remembered that the time units associated with dispersal, extinction, and evolutionary rates correspond to large lengths of time. Parameter values were chosen that compromised parameter space sampling with computer time and storage limitations. For example, combinations of parameter values that allowed the size of phylogenies to exceed five hundred were avoided. It was not at all clear when the simulations should be halted; In time, the original contiguous land mass would break up into a fine dust and support no diversity at all. An arbitrary decision was made to stop the program shortly after the appearance of the fourteenth island. For the parameter values sampled here, it was not uncommon to see the total number of extant species peak and begin to drop off toward the end of the one hundred units of "geological" time (see fig. 11.3).

When a population of a particular species undergoes speciation, its evolutionary trajectory through niche space becomes decoupled from that of populations of its former conspecifics, and it will drift randomly (or shift in accordance with local interspecific competition should it be sufficiently intense) through the two-dimensional niche space. There is, however, no arbitrary shift of its niche coordinates purely as a result of speciation per se, although it is very likely that subsequent divergence will occur. This assumption is in contrast to other published work of this type (e.g., Endler 1982; Colwell and Winkler 1984; Raup and Gould 1974). Our model considers many fewer characters (be they morphological, behavioral, or whatever), and we assume that the cause of reproductive isolation lies in some other "dimension" of the population.

That species may under some conditions of low competition wander randomly around niche space is not to assume that populations are not exposed to directional selection processes. The simulation implicitly assumes the existence of *local* selection forces other than interspecific competition, which, over the scale of geological time, will not be unidirectional. Thus conditions are homogeneous on each island but implicitly heterogeneous over the archipelago.

For convenience, this simulation is presented in the context of an island archipelago developing over a very long period of time. It could easily apply to any sort of large-scale, long-term fragmentation of habitat. An important additional assumption is that the gross biology of the taxa under consideration does not evolve; it is assumed that the probability of dispersal over specified distances remains constant throughout the simulation, as does the probability of the population going extinct under specified interspecific conditions on islands of a particular size. Although these assumptions are not completely true, we believe they are not unreasonable when considering such disparate taxonomic groups as snails, lizards, finches, gulls, etc. Our model can be thought to operate over any taxonomic scale within which these constraints are met.

The ecological functions ($D(d_{i,j})$, $C(i, x, y)$, $E(a_i, s_{ij})$) describe only the numerical properties of the functions without implying any causal process. Therefore, low extinction rates could be due to inherent properties of the population dynamics of the species (e.g., good bottlenecking ability: Roughgarden 1986), the nature of the environment, or maybe some interspecific interaction other than competition. Dispersal probabilities could derive from the spatial scale of the vicariant process or the vagility of the taxa. The extent of competition could be the result of differences in niche width, "keystone" predation (Paine 1966), or the absence of resource limitation.

It should be apparent from the description of the model that the extent to which competition occurs on the islands is not directly controlled. The parameter q determines the intensity of competition between two sympatric species separated by a given distance in niche space (but makes no assumptions as to the nature of the competition or how the species arrived at their respective positions). This parameter also plays a critical role in determining whether or not a species can successfully colonize an island (through T_{ex}), the probability of extinction (through $E(a_i, s_{ij})$) and the evolutionary trajectory through niche space. The parameter q is instrumental in the generation of diversity over the entire developing archipelago, but only indirectly influences the overall frequency of competitive interactions or the importance of competition in determining the nature of the resultant communities.

The function $N(a_i)$ relating island area to available niche space on island i has no empirical basis. It only assumes that new niche area is added progressively more slowly as island area increases. Niche space is assumed to be circular, and the carrying capacity is assumed constant at all points under the resource distribution. It follows from this assumption that the risk of extinction is not *directly* dependent on a species' position in niche space.

The map of the archipelago over one hundred vicariant time units is illustrated in figure 11.1. The area cladogram corresponding to the development of the archipelago is shown in figure 11.2 together with the island sizes.

Combining the function $N(a_i)$ with $C(i, x, y)$ (the function describing the extent to which species compete in niche space) and T_{ex} allows calculation of a theoretical ceiling on diversity. Assuming species are distributed evenly over the niche space available on each island at a sufficient density that the level of competition for all re-

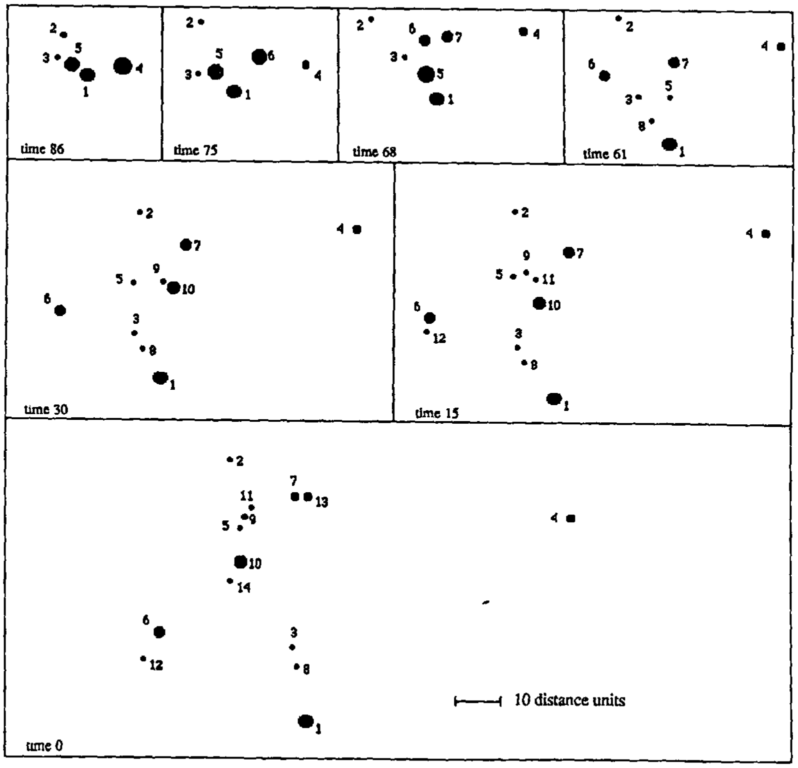


Figure 11.1 Map of the archipelago through geological time (100 time units ago to present). All diagrams are to the same scale. Size of island marker is approximately proportional to island area.

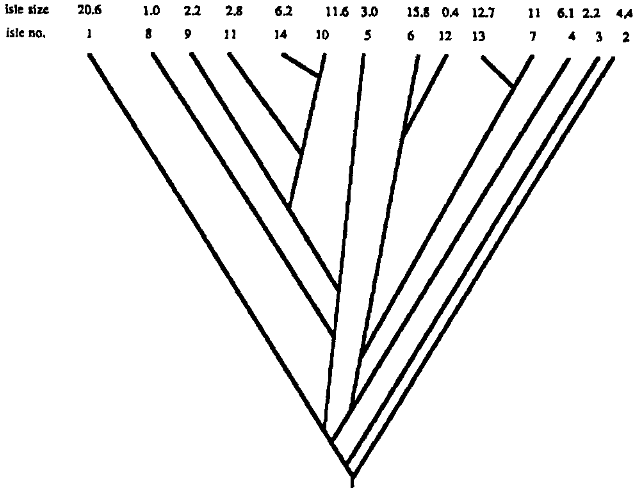


Figure 11.2 Area cladogram of the archipelago, with island sizes. Bifurcations are marked on a vertical scale of 100 time units.

sources just exceeds T_{ex}, then the island is invasion-proof to further immigrants, and an upper limit on the number of species supported by the island can be calculated. If this calculation is carried out for all the islands in the archipelago at different times in its development, and if endemism is assumed to be 100%, then one arrives at the total possible diversity, as illustrated in figure 11.3. Overlaid on the graph are typical curves for the buildup of extinct and extant species and the timing of the thirteen vicariant events.

Procedure

Different seeds were used for different random processes (i.e., vicariant and ecological processes). By holding the seed responsible for the generation of the random archipelago constant, the vicariant history was made identical for all simulations. Each simulation yielded a complete record of the biogeographical history of the archipelago with respect to predefined levels of extinction, dispersal, and competition. One simulation was performed for each combination of extinction (c = 0.5, 0.9, 5), dispersal (k = 0.1, 0.5, 0.75, 1, 10) and competition (q =1, 0.5) parameters. In order to investigate the influence of chance on these simulations, ten additional runs were performed for *each* combination of extinction and dispersal parameters with an intermediate level of competition: q = 0.75, c = 5, 0.9, 0.5; k = 0.1, 0.5, 0.75, 1, 10, changing only the seed responsible for nonvicariant events. The program was written in Pascal and run on a Sun 4 computer. Each run lasted from 1 to 30 hours, depending on the parameter settings; a total of 2000 hours of computer time was expended.

Sharpening the Concepts

For the purposes of clarity and conciseness, we will restrict the meaning of certain terms to particular aspects of the model. By *history* we mean the geological vicariant history of the islands (age, ancestry, and physical positions through time). The *effects of history* are defined as the detectable imprint of history on specified aspects of the biota of the archipelago. *Chance* is the phenomenon whereby a particular event with a specified probability occurs or does not. The *effects of chance* are those that result from changing the sequence of random numbers that the computer uses to determine the occurrence of chance events (*not* the probability of the events themselves). *Ecology* is restricted to the vagility, extinction, and competi-

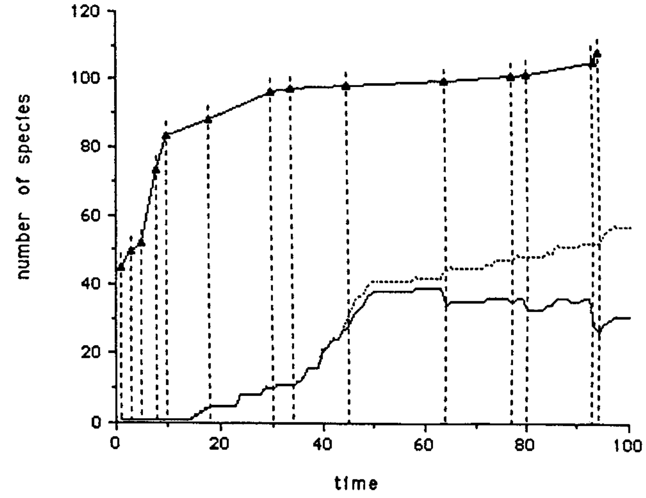


Figure 11.3 The theoretical upper limit to species diversity changes with the development of the archipelago. The curve shown (triangles) is for a taxon prone to high levels of interspecific competition (the curves for low and medium competition are exact multiples of this). The lower two curves illustrate gamma diversity (solid line) and the total number of species evolved (dotted line) for a highly competitive, highly vagile taxon that has a low extinction probability. The thirteen vicariant events (dashed lines) are superimposed on the graph.

tion functions of the species (outlined in table 11.1). The *effects of ecology* are those that result from changing the parameters in the aforementioned functions. In this model, history is fixed, ecology and chance are variables. The *effects* of history, chance, and ecology on one another and on the emergent biota are a complex interplay of the three phenomena.

The model clearly recognizes a "geological" time scale and an "ecological" time scale through the ratio of V_T: E_T. By manipulating these two constants, emphasis can be placed on geological or ecological time as required. For computational convenience, it is useful to make E_T moderately small and to increase dispersal and extinction probabilities and evolutionary rates accordingly (for example, by decreasing E_T from 1000 to 1 and increasing the probability of extinction from 0.00001 per year to 0.01 per 1000 years). This procedure does not affect the mean number of times such probabilities are realized, but it does affect the variance around the mean (a major focus of this study). Difficulties of integrating ecological and geological time are severe (Ricklefs 1989b). The manner in which the "paradox" between these time scales is resolved is likely to have a significant impact on the results obtained from such models. The problem, however, is not easily addressed in our model, because changing E_T would certainly change the random number sequence; any subtle trends would then be difficult to distinguish from those of chance.

RESULTS

The Effects of Ecology

The total number of species extant over the entire archipelago (gamma diversity) for different parameter settings is illustrated in figure 11.4. The gamma diversity behaved much as expected, being highest at intermediate vagilities. There were, however, some occasions when an increased rate of extinction resulted in higher gamma diversity. When levels of endemism are sufficiently low, a high *local* extinction rate *could* vacate niche space on an island, enabling additional dispersal-speciation events that would result in the generation of a higher number of species over the whole archipelago. When endemism is at a very high level (mostly very low vagility taxa), local extinction is often accompanied by global extinction, and the above explanation is insufficient. These cases, however, show rather high coefficients of variation (see fig. 11.11), and chance alone could account for them.

Faunal diversification occurs either through vicariance and subsequent speciation of island faunas or through interisland dispersal and subsequent speciation. Dispersal probabilities decrease exponentially with distance between islands, but speciation only occurs after the probability of dispersal drops below T_S. There is, therefore, a limited range of interisland distances, falling within a relatively narrow "window," in which dispersal is at all likely and speciation possible. Island pairs whose distance from each other lies within these windows are likely to experience a local proliferation of species resulting from reciprocal dispersal and speciation (we call this the "ping-pong" effect).

For taxa of very low vagility, these windows will probably occur only between islands that have recently split; Hence, there will be relatively few such windows. For taxa of very high vagility, these windows will occur only between the most distant islands—of which there are also relatively few. But for taxa of intermediate vagility, there may be many such island pairs over geological time, allowing for much greater diversification. It follows that pairs of islands drifting apart may move through a window corresponding to a lower-vagility taxon and then, at some later time, move through the window corresponding to a higher-vagility taxon. The archipelago thus nurtures the proliferation of taxa with different vagilities at different stages of its geological development. Alternatively, archipelagoes with very different histories could generate equivalent sequences of such windows for very disparate types of taxa. Similarities in ecological and biogeographical patterns may emerge as a result of corresponding ratios of vagility to vicariant spatial scale, and not necessarily from any taxonomic proximity of the study organisms. Diversity is not a function of vagility alone, but is influenced by the creation of these speciation windows, and this is the probable explanation for the approximately equal gamma diversity of the taxa with low, medium, and high vagilities.

Total diversity (extant + extinct species) behaved similarly to gamma diversity with respect to vagility, but increased with extinction proneness (fig. 11.5). High extinction rates generated increased species turnover rates, vacating niche space for additional dispersal-speciation events. From figures 11.4 and 11.5, we see that, although taxa prone to high extinction rates are more proliferous, taxa prone to low extinction rates have higher extant diversity. (Note that, in the interests of clarity of graphic

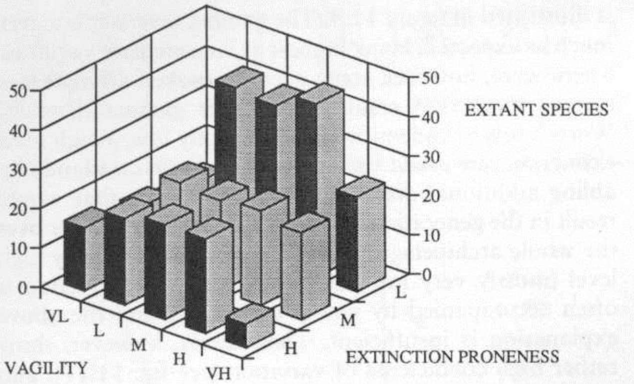


Figure 11.4 Mean gamma diversities for taxa of medium competition proneness. For taxa of very low (VL), low (L), medium (M), high (H), and very high (VH) vagility and high (H), medium (M), and low (L) extinction proneness.

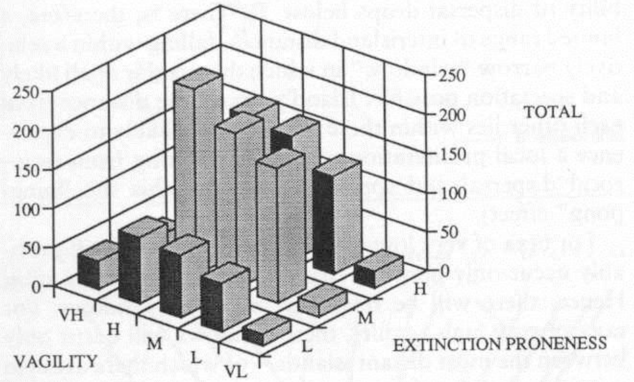


Figure 11.5 Mean total diversities (extinct + extant species) for taxa of medium competition proneness. (Abbreviations as in figure 11.4.)

presentation, the orientation of the horizontal axes are frequently reversed in the figures.)

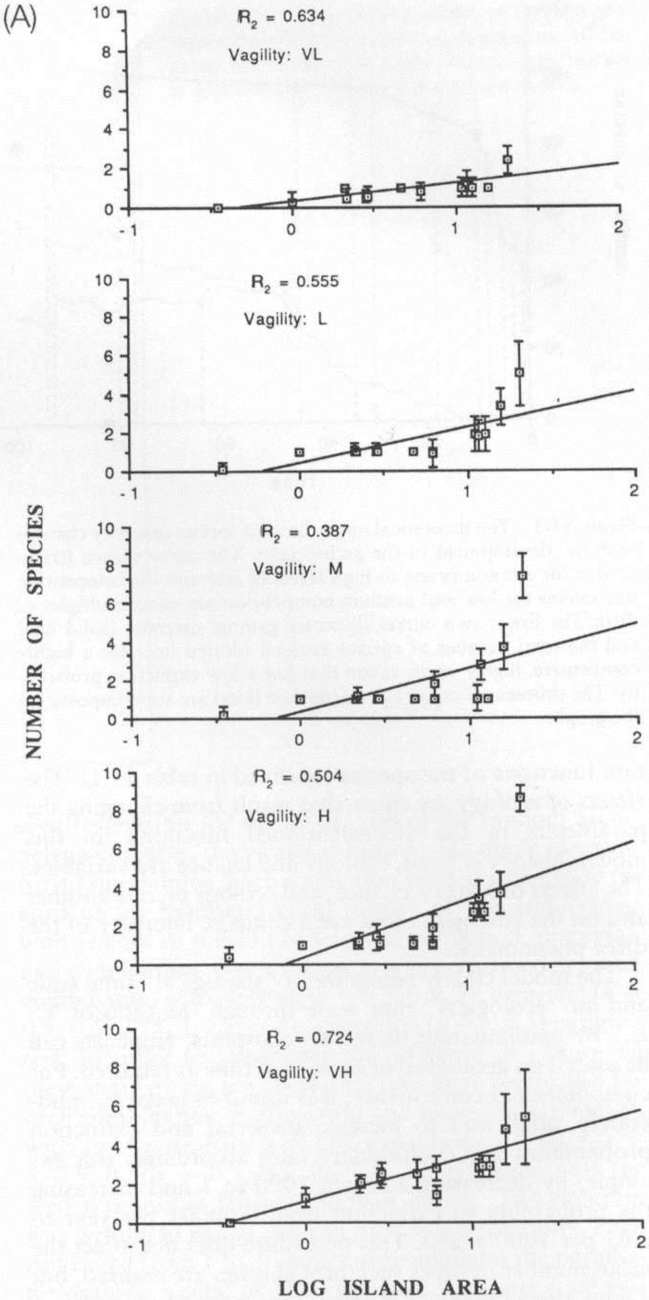
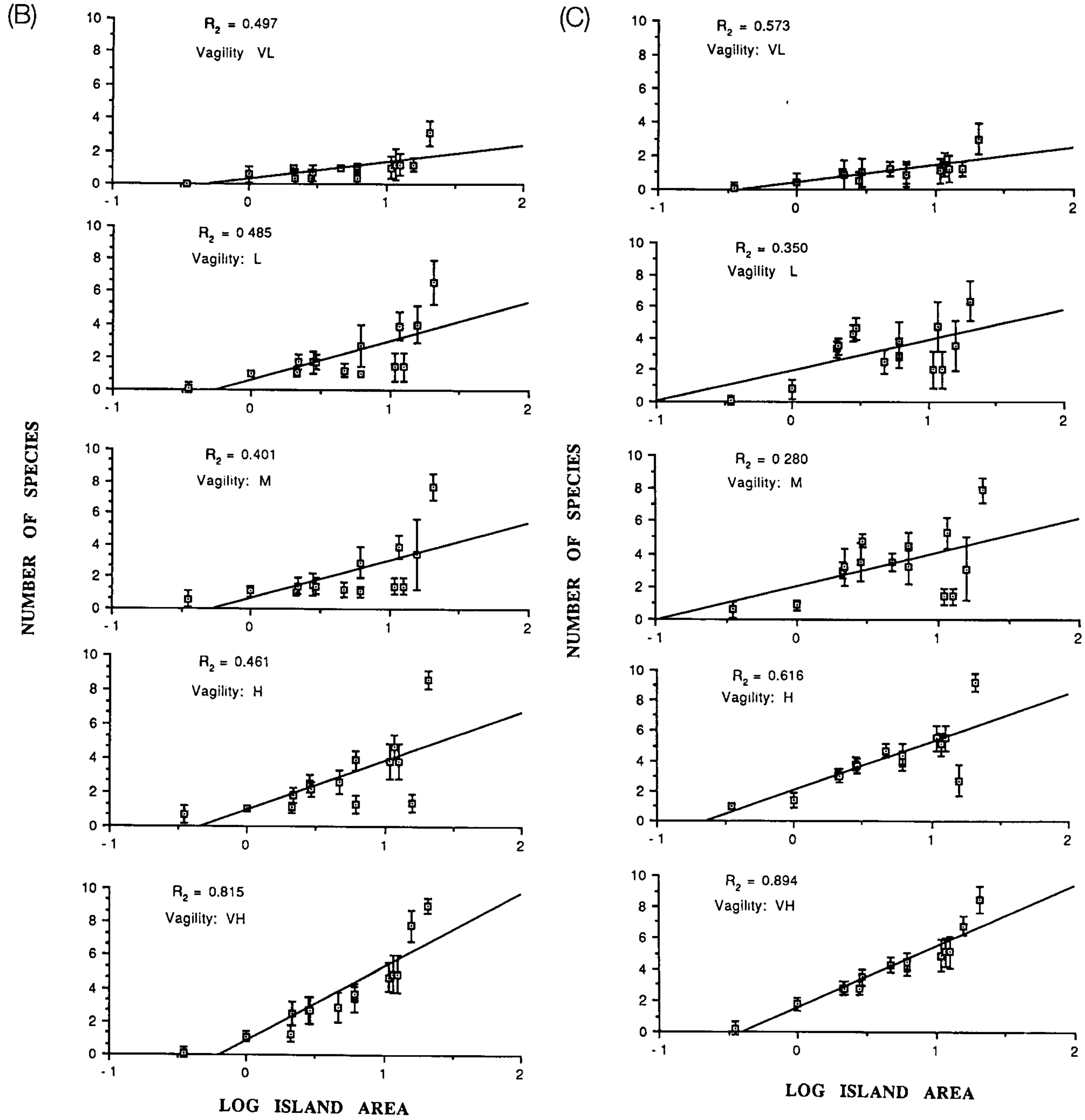


Figure 11.6 Species diversity (alpha diversity) plotted against the log of island area for taxa prone to medium levels of interspecific competition and to (*A*) high, (*B*) medium, and (C) low levels of extinction. Each point is the mean of ten runs in which all parameters were kept constant except for the seed used to determine the sequence of random numbers. One standard deviation is shown on either side of the point. Scanning down each column, the vagility increases from very low (VL) through low (L), medium (M), high (H), to very high (VH).

Alpha diversity was defined as the number of species on each island. Because larger islands have a greater total niche area, we expected larger islands to support more species. Given the arbitrary assignment of constants to the function relating niche space to island area, N(a_i), no particular mathematical relationship between local alpha diversity and area was expected, however. Figure 11.6 shows the observed species-area relationship plotted semilogarithmically. Each point is the mean of ten runs; one standard deviation around each point is shown. The slope of the least squares fit steepens with increasing vagility at all three extinction settings, which is indicative of the progressively more influential role of the larger islands in "housing" the diversity of the archipelago. This suggests that taxa with higher vagilities may exploit the additional niche space on larger islands more efficiently than do lower-vagility taxa. The goodness of fit is worst at intermediate vagilities (maximum gamma diversities). The percentage of endemic species varied from 33% for very high vagility, high-extinction, low-competition taxa to 100% for almost all very low vagility taxa. Beta diversity was defined as gamma diversity divided by mean alpha diversity over the fourteen islands (Whittaker 1972). Thus, beta diversity behaves very similarly to percentage of endemic species (fig. 11.7). As expected, beta diversity decreased with increasing vagility. For reasons similar to those discussed above, we expected a positive correlation between extinction rates and beta diversity, especially



when endemism levels are low; however, proneness to extinction had virtually no effect on beta diversity.

Attempts to control the severity of competition in the simulations were largely unsuccessful due to compensatory adjustments in diversity. The process of diversification merely acted to fill up the niche space until a high level of competition inhibited it from doing so further; this required a higher species density when species' competitive capabilities were low than when they were high. It would seem that attempts to create low levels of competition in communities created this way are bound to fail if competitive constraints are imposed on a "per species" basis. The competition parameter could only be used as an indirect control of species diversity.

The Effects of History

Chance, history, and ecology all combine to mold the size and topology of a taxon's phylogeny. On its own, the phylogeny provides no historical information. In combination with data on species distributions or elements of geological history, however, phylogenies are powerful and essential tools for analyzing the effects of history on the evolutionary development of any particular biota. An index quantifying the influence of history should obviously be related to the amount of historical information present in the distributions of species over the archipelago and be proportional to the accuracy with which the geological history can be reconstructed from biogeographical information. Our data were analyzed for the presence of historical impact in two different ways. The first assumes complete knowledge of the geological and biological history, the second, only the phylogeny and distributions of the species on the islands.

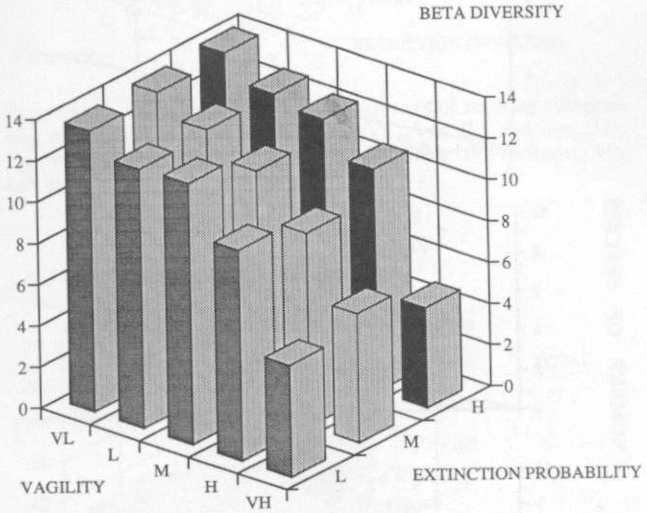


Figure 11.7 Mean beta diversities over ten runs with different seeds for taxa of medium competition proneness. (Abbreviations as in figure 11.4.)

If the island cladogram and the distribution of species on the islands are fully known, then the importance of history in shaping the phylogeny will be reflected in the substantial intersection between sets of species formed by the union of species assemblages on islands belonging to the same "geological" clade, and sets of species belonging to a phylogenetic clade. Figure 11.8 and Table 11.2 demonstrate the development of an index that measures the degree of concordance between the island area cladogram and a given phylogeny. Figure 11.9 shows the application of this index to the phylogenies resulting from replication at medium levels of competition. Each bar is the mean of ten simulations and represents the concordance above and beyond that expected to occur by chance alone. Observed concordances vary between 20% and 96% above expected values (i.e., those expected to occur if species were distributed randomly over the islands). In general, historical constraints become more important as vagility decreases and extinction rates increase. High extinction rates (resulting in a modern extant fauna) have the effect of continually updating the relationship between geological past and biogeographic distributions, eliminating the influence of "deep history" but deepening the imprint of more contemporary history.

In practice, an accurate vicariant history is rarely available; when this is the case, an alternative indication of historical constraint would be a higher-than-expected relatedness between sympatric species. Accordingly, the mean relatedness (as measured by the number of nodes between two species on the phylogeny) was calculated between all extant sympatric species pairs on each island, and then

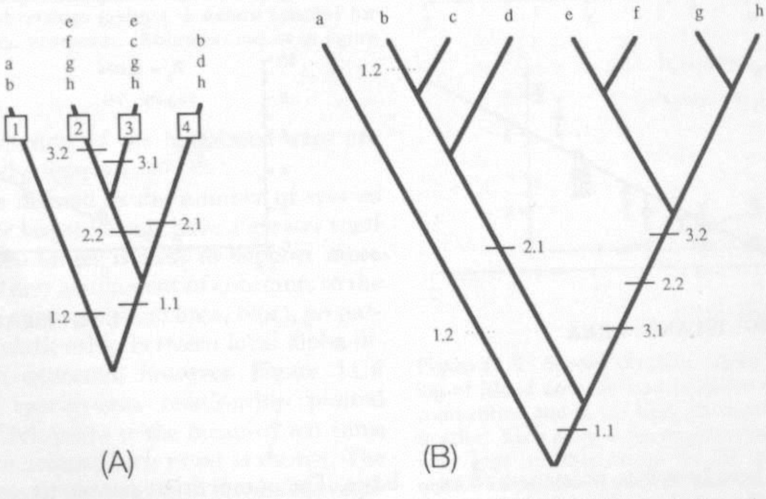


Figure 11.8 Calculation of a concordance index (*H*) between area cladograms coupled with species distributions and the species' phylogenies for a hypothetical data set. (A) Area cladogram for four islands (1–4). Species present on each island are indicated at the termini (a-h). Six area clades are denoted (1.1–3.2). (B) Species represented in these six area clades are "mapped" onto the known species phylogeny. The objective is to match sets of species represented in area clades with sets of species constituting clades within the known species phylogeny, and to establish to what extent the similarity of each pair of sets exceeds that expected from a random distribution of species on islands. For each of the six sets formed by the union of species assemblages of islands belonging to area clades (1.1–3.2), the species phylogeny is scanned for the species clade containing the most similar set of species. These "most similar" clades are indicated on the known species phylogeny (by a dotted line when there is more than one "most similar" clade.) The similarity of the sets to each other is quantified using Sorenson's index (Pielou 1969) (see table 11.2). Because the size of the species pool is known, one can also calculate analytically the expected value of Sorenson's index for two sets of known sizes if the sets were assembled randomly from the species pool. These observed and expected values of concordance are averaged over all clades, and the ratio between them is taken as an estimate (*H*) of historical constraint on the species' biogeographical distributions. In this example, the concordance between the island cladogram and species phylogeny is 30.5% over what would be expected by chance alone, indicating a substantial degree of historical constraint.

Table 11.2. Calculation of Observed and Expected Sorenson's Index

Clade	Spp. common to both clades	Spp. unique to area clade	Spp. unique to phylogenetic clade	Observed Sorensen's index	Expected Sorensen's index
1.1	7 (b,c,d,e,f,g,h)	0	0	1.000	0.877
1.2	1 (a), or (b)	1 (b), or (a)	0	0.667	0.667
2.1	2 (b,d)	1 (h)	1 (c)	0.667	0.523
2.2	4 (e,f,g,h)	1 (c)	0	0.889	0.603
3.1	3 (e,g,h)	1 (c)	1 (f)	0.750	0.571
3.2	4 (e,f,g,h)	0	0	1.000	0.571
			Means	0.829	0.635

Note: Calculations for hypothetical data set presented in figure 11.8.

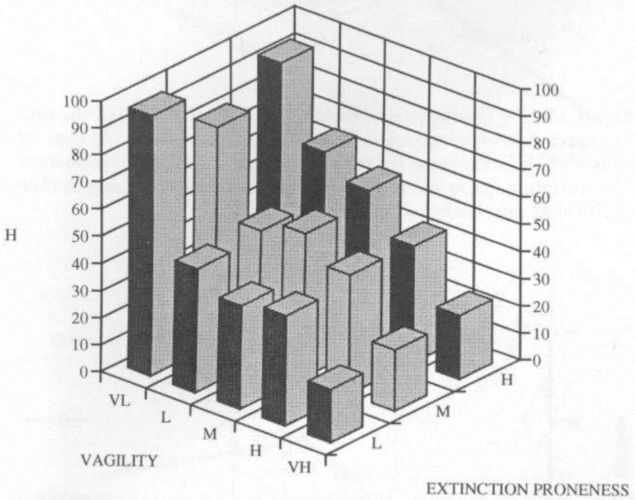


Figure 11.9 Mean concordance indexes (*H*, see figure 11.8) over ten runs with different seeds for taxa of medium competition proneness. (Abbreviations as in figure 11.4.)

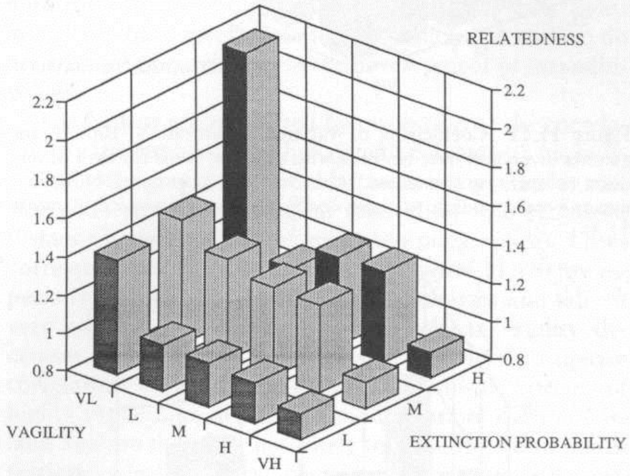


Figure 11.10 Mean ratios of expected to observed relatedness of sympatric species (R) over ten runs with different seeds for taxa of medium competition proneness. (Abbreviations as in figure 11.4.)

this quantity was averaged over the entire archipelago. The ratio of this figure to the mean relatedness of all extant species pairs inhabiting the archipelago was taken as an index of historical constraint. When the index is greater than 1, it implies that sympatric species are more closely related to each other than expected; when it is less than 1, sympatric species are less related than expected. It is evident from figure 11.10 that this measure is not as sensitive to the ecological context as is the concordance index. The broad trends shown by the two measures are, however, entirely consistent, despite the use of less information in the relatedness index. It appears that by taking into account the geological ancestry of the islands, the concordance index is made more sensitive to subtle associations in species distributions arising from long past geological associations.

Various idiosyncrasies in the biogeography of this archipelago, attributable to history, can be observed by matching the species-area relationships (see figure 11.6) to the map of the archipelago over time (see figure 11.1). For example, the largest island (island 1) consistently floats above the predicted alpha diversity; for low extinction rates, the second largest island (island 6) is often found substantially below the predicted diversity. The two most recent islands (13 and 14) often fall below the predicted diversity. These idiosyncrasies reflect the predictable effects of island isolation, size, and age on biogeography, as developed by MacArthur and Wilson (1967).

Effects of Chance

The effects of chance on the output of the simulations were assessed in terms of the standard deviations (SDs) and coefficients of variation (CVs) surrounding the means of the variables of interest. Figure 11.11 illustrates how the CVs around the mean gamma diversities vary with the ecological parameters. Chance has the greatest influence (CVs around 20%-35%) on those taxa with very low and very high vagilities; the effect is enhanced at the extremes of extinction proneness. These parameter settings correspond to those communities with a natural tendency to low diversities.

In contrast, chance had a relatively low impact on beta diversity. The CVs surrounding the means illustrated in figure 11.7 never exceeded 7.9%, except in the case of the high-extinction, very high vagility taxa, whose CV was 33.7%. The impact of chance on alpha diversity and the species-area relationship can be seen from inspection of the error bars (representing one standard deviation each way) on the graphs presented in figure 11.6. There are no very clear or simple patterns: some islands seem to be particularly vulnerable to the effects of chance (for example, the second largest island), while others are very predictable (many of the intermediate-sized islands). The error bars are broadest at intermediate vagilities (corresponding to the highest gamma diversities).

Chance not only affects the observed ecological pat-

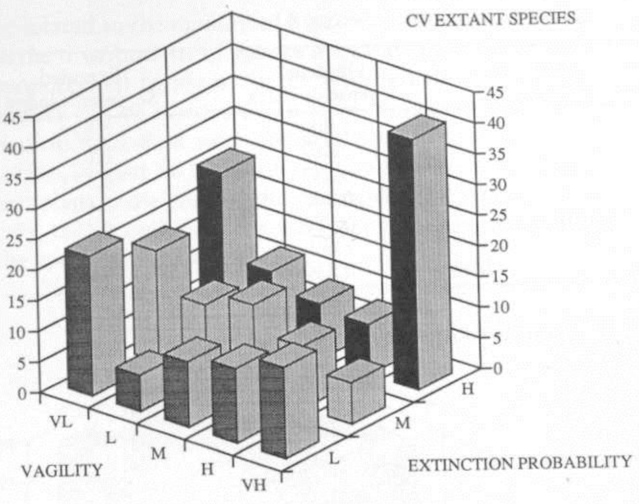


Figure 11.11 Coefficients of variance (SD/mean × 100) of the gamma diversities over ten runs with different seeds for taxa of medium competition proneness. (Abbreviations as in figure 11.4.) The means corresponding to these coefficients are illustrated in figure 11.4.

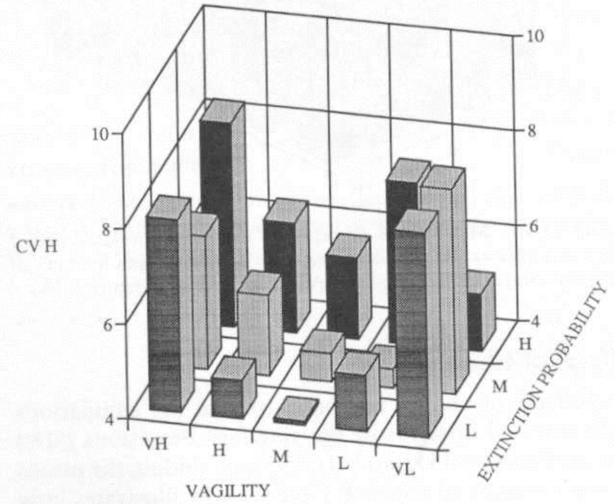


Figure 11.12 Coefficients of variance (SD/mean × 100) of the concordance indexes (H) over ten runs with different seeds for taxa of medium competition proneness. (Abbreviations as for figure 11.4.) The means corresponding to these coefficients are illustrated in figure 11.9.

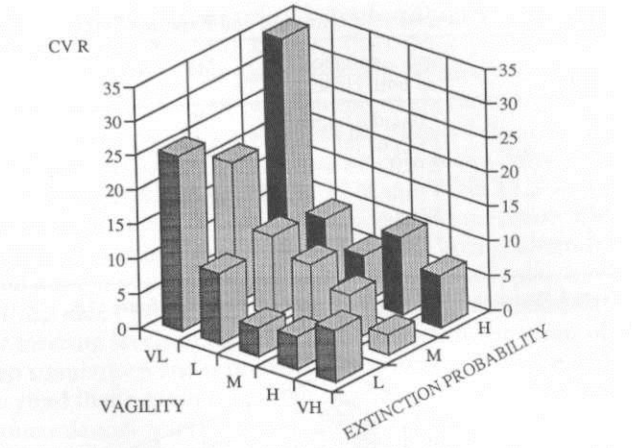


Figure 11.13 Coefficients of variance (SD/mean × 100) of the ratio of expected to observed relatedness of sympatric species (R) over ten runs with different seeds for taxa of medium competition proneness. (Abbreviations as in figure 11.4.) The means corresponding to these coefficients are illustrated in figure 11.10.

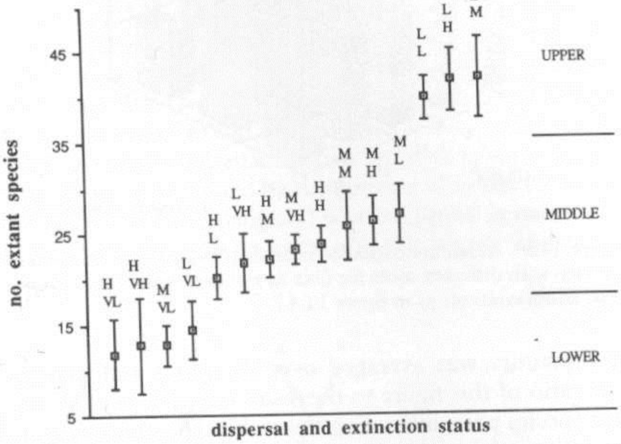


Figure 11.14 Mean gamma diversities of taxa of medium competition proneness with one standard deviation plotted on each side of the mean for the 15 different combinations of vagility and extinction proneness (each replicated ten times). Abbreviations as in figure 11.4: the top abbreviation corresponds to the level of extinction proneness; the lower, to the level of vagility.

terns but could also affect the imprint of history. Figure 11.12 illustrates the coefficients of variation around the mean values of the concordance index presented in figure 11.9. The percentages are all impressively low (2%–8%), yet there is a well-defined "valley" carved into the surface at intermediate parameters. In contrast, the CVs around the mean values of the expected: observed relatedness ratios (figure 11.3) decline almost monotonically from quite high levels (20%–30%) for the low vagilities down to the very high vagility taxa (3%–5%).

Figure 11.14 shows that for the fifteen different combinations of vagility and extinction proneness, there are only three readily distinguishable levels of gamma diversity. The three taxa among the group with the highest gamma diversity are all of low extinction proneness with low, medium, and high vagilities. The two groups with lower gamma diversities are composed of an apparently miscellaneous combination of vagility and extinction proneness.

Evolution

Figure 11.15 illustrates the temporal development of phylogenies embedded in the two-dimensional niche space for three values of vagility at intermediate extinction rates. The phylogenies illustrate two major features. First, there is a high degree of variability in lineage stasis with time. The very low vagility taxa demonstrate very erratic and convoluted evolutionary trajectories through time. A high percentage of endemism coupled with a low density of species packing results in a measure of "freedom" with

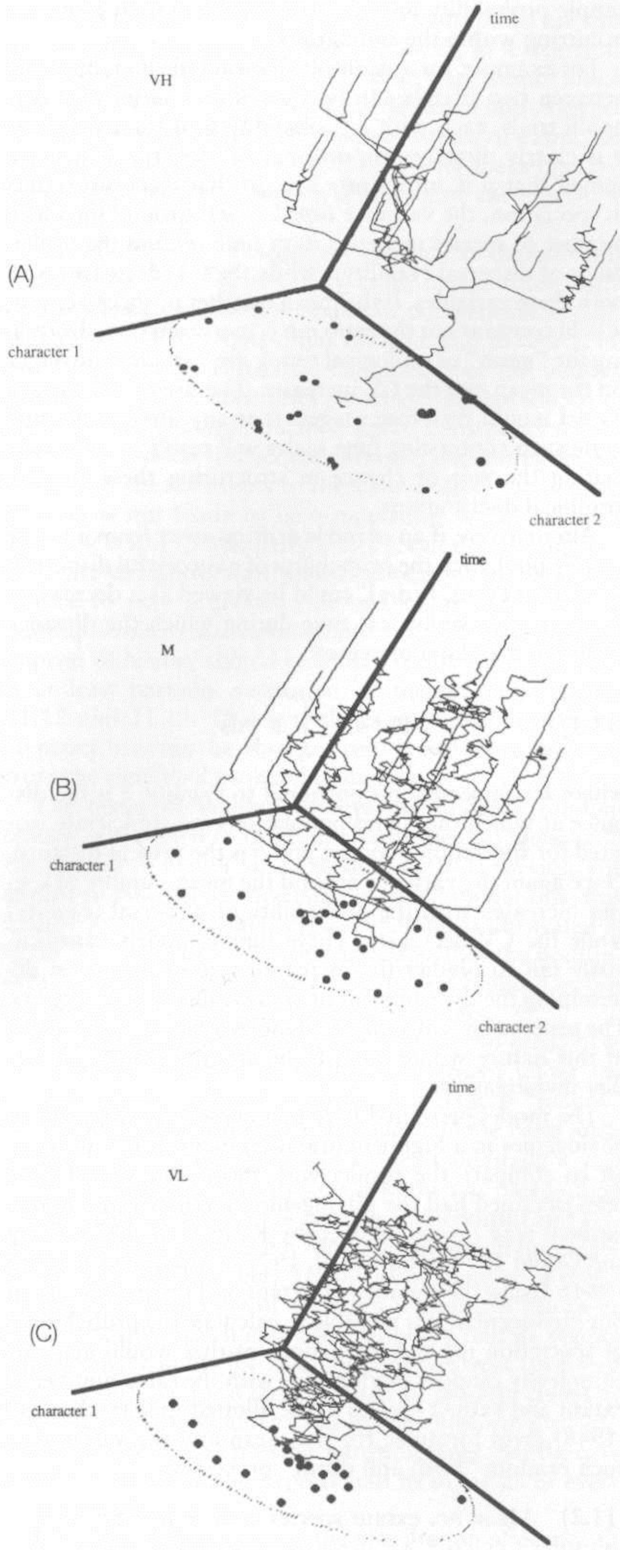


Figure 11.15 The temporal development of phylogenies (extant species only) embedded in the two-dimensional niche space. The "shadows" of the tips of the phylogenies are shown on "floor" of the graph. The dotted circle delineates the niche space available on the largest island (island 1). VH, very high vagility; M, medium vagility; VL, very low vagility. The phylogenies correspond to taxa prone to medium levels of competition and extinction.

which to respond to the local conditions. At intermediate vagilities, the systems become more diverse, and "wandering" of a lineage is confined by the presence of interspecific competition. At very high vagilities, gamma diversity drops off, but the trajectories are stabilized by the fact that endemism is now at a very low percentage, and gene flow from other islands (on which conditions may be quite different) inhibits local response to changing conditions.

The second feature is the general level of "bushiness," which results from the geography becoming conducive to speciation at different times for taxa with different vagilities. For low-vagility taxa, speciation starts and continues with each vicariant event. At high vagilities, such "windows" for high speciation rates (as referred to earlier) do not open until much later in the development of the archipelago.

These ideas are supported by inspection of the correlation coefficient between phylogenetic relatedness (as measured by the number of nodes between any particular species pair) and morphological separation (the euclidean distance between a pair of species in niche space). These correlation coefficients (illustrated in figure 11.16) are especially high for very high vagility organisms and fall off very steeply to surprisingly low levels as vagility decreases. This relationship arises as a result of the negative correlation between vagility and endemism. Species of highly vagile taxa are often found on more than one island and are therefore less likely to be subjected to unidirectional selection. Rapid character divergence away from sister species is unlikely to occur under these circumstances, resulting in a higher correlation between phylogenetic relatedness and morphological separation. When most species are endemic, there is no such inhibition on the evolutionary trajectories, and the correlation is substantially weakened.

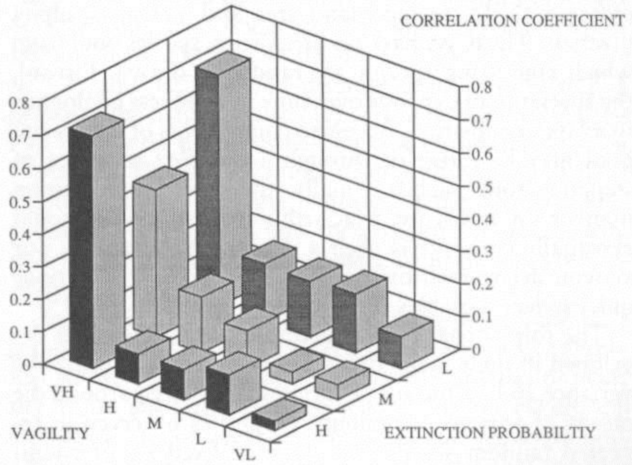


Figure 11.16 Mean correlation coefficients between phylogenetic "relatedness" as measured by the number of nodes between any particular species pair, and morphological separation, as measured by the euclidean distance between a particular pair of species in niche space for taxa prone to medium levels of competition (each replicated ten times).

DISCUSSION

The well-known equilibrium model of MacArthur and Wilson (1967) addresses the effects of static physical factors and current ecological conditions on species diversity and distributions. Species diversity patterns are a result of the effect that physical factors, such as island area and isolation, have on the probability of colonization or extinction of species derived from a mainland pool. Because local conditions are island-specific, colonization and extinction probabilities are unique to each island. Using the intuitively simple idea that ecological conditions cause colonization rates to decrease and extinction rates to increase with species number, an equilibrium species number is predicted for each island.

We have employed much of the same simple logic as MacArthur and Wilson did in designing the dynamics of the events that take place over our ecological time scale. The functions used to determine whether species successfully colonize mimic the assumptions of the equilibrium model. The probability of successful island colonization decreases directly with distance and indirectly with island area. The decrease with area and number of resident species (alpha diversity) is implicit because, as area decreases and alpha diversity increases, the probability that an island contains invadable niche space also decreases. In addition, the probability of extinction increases directly with a decrease in island area.

There are, on the other hand, some important differences between the fundamentals of our model and the equilibrium model. First, because the ecological events are embedded within a broad geological time scale, components of the MacArthur-Wilson model that are held constant become variables in our simulations. This nested structure allows us to see how drastically the dynamical nature of the equilibrium model overwrites the effects of history. Second, by assuming that a species requires a fixed proportion of two-dimensional niche space, we are specifically defining why colonization probabilities decrease with decreasing island area and increasing alpha diversity. Third, we have no preexisting species pool from which colonizing species are randomly drawn. Instead, the species pool expands over time in a process analogous to adaptive radiation. Access to components of the species pool may be direct or through a complex sequence of stepping-stone islands. Finally, the equilibrium species number on which the MacArthur-Wilson model should eventually converge is itself a dependent variable in our system, determined by a complex interaction of various independent variables.

The role of chance in structuring the communities developed in these simulations has been assessed using the variance and coefficient of variation generated around the means of various community properties observed in repeated random simulations under a fixed set of conditions. Of particular interest were the conditions under which chance might be expected to be more or less important. Purely statistical processes may explain the observed trends in the variance and coefficient of variation; these may be suggested by the construction of extremely simple probability models that emulate certain processes occurring within the simulations.

For example, for any one geological time unit, dispersal between two islands can be viewed as a series of n Bernoulli trials, each with a probability p of success (where p is clearly directly proportional to vagility). If it is assumed that p is sufficiently low so that dispersal results in speciation, the variance ($np\{1 - p\}$) around the mean number of species increases with time (n) and the probability of dispersal (vagility), while the CV decreases with both these variables. If the mean number of successes (np) is held constant but the ratio $n{:}p$ is increased (i.e., decreasing the "grain" of ecological time), the variance converges on the mean and the CV increases. The use of this type of model would therefore suggest that any attempt to integrate such contrasting time scales will result in underestimating the role of chance in structuring these biogeographical distributions.

Alternatively, if an island is drifting away from a major species pool, then the probability of a successful dispersal-speciation event, P{d-s}, could be viewed as a decreasing function over geological time during which the distance (s) to the mainland increases:

$$\text{(11.1)} \qquad \mathrm{P(d\text{-}s)} = \int_a^b e^{-ks}\,ds$$

where k is inversely proportional to vagility, a is the distance at which the island populations are sufficiently isolated for speciation to occur, and b is the present distance. Once again the variance around the mean number of species increases with the probability of dispersal (vagility) while the CV decreases. These simple models conspicuously fail to predict the increased role of chance in determining the distributions of taxa with very high vagility. The generation and analysis of more sophisticated models of this nature would seem to be an area worthy of further investigation.

The model presented here permits the development of phylogenies in a highly nonrandom manner. It is of interest to compare the results with those that would have been obtained had the phylogenies developed in a purely random way (as exemplified by Raup et al. 1973; Raup and Gould 1974; Gould et al. 1977; Colwell and Winkler 1984). Using the number of extant and extinct species in our phylogenies, it is possible to calculate the probabilities of speciation (ρ) and extinction (ε) that would generate completely random phylogenies with the same number of extant and extinct species in the allotted time (τ). Kendall (1948) gives formulae for the mean and the variance of such random "birth and death" processes:

$$\text{(11.2)} \qquad \text{Mean no. extant species} = (1 + \rho - \varepsilon)^{\tau}$$

$$\text{(11.3)} \qquad \mathrm{var} = \frac{\rho + \varepsilon}{\rho - \varepsilon}\, \varepsilon^{(\rho - \varepsilon)^{\tau}} \left(\varepsilon^{(\rho - \varepsilon)^{\tau}} - 1\right)$$

The means are by definition the same, but the coefficients of variation of the random process (which we have found to be typically 100%–120%) are consistently five to twenty times greater than those of the process that generates the phylogenies in our model. This suggests that the processes producing faunal buildup in our model are subject to some negative feedback, resulting in a degree of convergence above that expected from pure chance alone. Since the discrepancy between the observed and expected variances is greatest at intermediate values of extinction proneness and vagility, this is where the feedback operates maximally (i.e., at parameter settings that correspond to high gamma diversity).

The source of the negative feedback is undoubtedly competition. For low-diversity taxa, or for those high-diversity taxa for which interspecific competition is of little importance, the system has the potential to reflect, indeed amplify, the stochastic component of the buildup process. At higher diversities (or where interspecific competition is a regulating factor), added constraints on the stochastic process restrict the variance, preventing the reflection of chance events to the same degree. When competition is not likely to be a regulating factor, or when diversity is low (particularly if as a result of low vagility), there are straightforward statistical reasons for expecting chance to play a greater role in the process of faunal buildup. Under these circumstances of low feedback, the imprint of history should be most variable, and this view is at least partially supported by inspection of figures 11.12 and 11.13. This hypothesis may explain the discrepancy between the observed results and those expected from the simplified probability models.

The temporal buildup of diversity under a random scheme is expected to result in an exponential increase in the number of extant (and extant + extinct) species. The temporal buildup of diversity in our simulations was hardly ever exponential (a typical example is illustrated in figure 11.3) and this difference indicates that the nonrandom processes contributing to the faunal buildup in our model *are* distinguishable from random ones.

Recently, methods have become available to predict the approximate structure of phylogenies grown under the random scheme referred to above. If a clade is "picked" from a phylogeny containing n species and the basal node removed, one is left with two clades containing r and $n - r$ ($= s$) species. This process is known as partitioning and generates a partition of type $r - s$. Slowinski and Guyer (1989) have shown that for clades in which the terminal taxa are labeled, there are the same number of possible trees for each type of partition (except for the cases when $r = s$, in which case there are only half as many). This property holds for randomly grown trees (personal observation). So, for a large number of random clades of identical size, one would expect to see a uniform distribution of clades over all possible partition types (bar the case when $r = s$, when one expects half as many as in every other type class).

It is of interest to compare the distribution of partitions of clades from our model with the expected distribution had the phylogenies developed randomly. In order to assemble a sample size that would allow the statistical comparison of the observed and expected distributions, it was necessary to pool all the clades of a particular size generated from all the parameter combinations (a total of 180 phylogenies). The comparison revealed that clades consistently (and highly significantly) partition in a very unbalanced way (i.e., that partitioning of a clade resulted in a small and a large subclade many more times than one would expect). This result holds for clades of size 4 (the minimum in which such partitioning is meaningful) to 16 (the largest clades for which an adequate sample size was available). Unfortunately it was not possible to detect for what type of taxa this nonrandomness would be greatest because of the large number of clades required to carry out a statistically meaningful analysis. Whether this is a legacy of the region's geological history or a by-product of ecological interaction remains unclear. Guyer and Slowinski (1991) have recently documented empirical evidence confirming the prevalence of unbalanced clade structures in real phylogenies.

Inspection of the island cladogram (fig. 11.2) and the map of the developing archipelago (fig. 11.1) suggests that species found on some islands will have a greater potential to undergo adaptive radiation than those on others. This may be due to the differential proximity of neighboring islands or the frequency of vicariant events effecting a former land mass, both in combination with the biology of the taxon. Another possibility is that development of one phylogenetic clade competitively suppresses the proliferation of another. It will be a long time before enough real phylogenies are established to test this hypothesis empirically.

Using the model presented in equation 11.1, it is possible to illustrate the window effect discussed above. In our simulations, speciation was assumed to occur when the probability of conspecific immigration was reduced to below 0.1 per ecological time unit. This probability corresponds to a distance of $-\ln(0.1)/k$ and represents the near side of the window. If b is now assumed to be large, it is possible to estimate the distance (intermediate between $-\ln(0.1)/k$ and b) at which 80% of the mean number of dispersal-speciation events would have occurred. This figure will be the far side of the window. For the same values of k used in this simulation, the windows for taxa of very high, high, medium, low, and very low vagility become from 23.02 to 44.05, 4.6 to 8.81, 3.1 to 5.9, 2.3 to 4.4, and 0.23 to 0.44 distance units, respectively. A glance at the map in figure 11.1 confirms that the broadest and narrowest windows will only be encountered rarely, explaining the lower gamma diversity observed in these vagility classes. That the majority of the diversification should be compressed into these relatively narrow windows is an inevitable consequence of using an exponentially declining dispersal function.

Erwin (1981, 171) states that "an understanding of a group's vagility must be a forerunner to any biogeographical study." Unfortunately, the dispersal abilities of many organisms (especially over geological time scales) are still shrouded in considerable mystery (but see Diamond, 1987 and references therein). Erwin argues that "founderism" (sensu Mayr 1942) will be rare in nature because ". . . weather patterns, ocean currents, or other means of dispersal are not 'freakish' when viewed on the geological time scale or especially on the evolutionary-rate scale." Such a view is open to two interpretations. The first is that dispersal is not a stochastic process—if it *could* happen it always will (i.e., dispersal with probability 1.0 over a finite range of distances and 0.0 otherwise); this view would virtually eliminate the role of chance in the development of biogeographical patterns. Alternatively, it could suggest the use of dispersal functions that generate uniformly low probabilities of dispersal over a range of distances. This interpretation permits the influence of chance but results in the contemporary past increasingly masking the influence of deep history. Our particular dispersal function and its relationship to the speciation mechanism is the product of an especially blind grope. Clearly, we must understand the nature of "epic" dispersal before we can seek consensus in the ongoing debate over the role of history and ecology in biogeography.

We are not aware of any previous attempts to model biogeography in this way. It is not clear to us how much can be learned from simulations of this type; however, several lines of investigation appear worthy of further pursuit. First, there is some heuristic value to abstract simulations of this type in that they demand the encompassing of an array of processes and patterns about which fairly little is known, thus highlighting areas for future empirical investigation. They also help by suggesting answers to questions for which we will never be able to get definitive empirical answers; for example: Were the entire process of faunal buildup over an archipelago to occur again, what is the probability of obtaining a similar result? How reliable are the distributions of different sorts of organisms in reconstructing geological history? Even though we have only considered these biogeographical patterns one taxon at a time, in reality faunas and floras develop concomitantly (although various temporal displacements may occur). Trends for hypothetical taxa reported here should be compared to real biogeographical patterns (e.g., snails, lizards, and birds in the Caribbean). Finally, highly "tactical" versions of such models that simulate the biogeography of particular real areas, defining in the program a hypothesized geological history and species source pool's could easily be produced (snails, fruit flies, and birds in Hawaii or the Galapagos are obvious candidates). The output from such models could illuminate possible inconsistencies in proposed biogeographical "stories." The failure of such tactical models to explain observed species distributions could raise questions even more interesting than those that result from successful models.

CONCLUSIONS

In its entirety our model is complex; it is, however, composed of a set of simple and intuitively appealing concepts. The output of diversity measures, species-area relationships, niche packing structures, etc., are sufficiently consistent with reality to generate a measure of confidence in some of the less obvious results. The fact that different organisms are differentially impressionable to the array of forces molding ecological and biogeographical patterns is an important dimension of the analysis and interpretation of ecological data.

Analysis of this model suggests that the nature of the study organism has a profound impact on the visibility of the historical effect, differentially affecting the rates at which the impressions of deep and contemporary history are obscured. Empirical quantification of this phenomenon remains a substantial challenge. Chance is expected to play a greater role in determining the diversity of inherently low-diversity, less competitive, and less vagile taxa. The detection of nonrandom processes through the analysis of patterns is often a formidable task. Techniques remain relatively unsophisticated, and difficulties are compounded because of low sample sizes. Our results suggest that the processes of faunal buildup and phylogenetic development may not be accurately approximated by a random algorithm.

Gould has remarked: "And so ultimately, the question of questions boils down to the placement of the boundary between predictability under invariant law and the multifarious possibilities of historical contingency" (Gould 1989, 290). We suggest that in the context of biogeography, the placement of this boundary depends on the general characteristics of the taxon under consideration. Further studies like this one might offer promising initial leads in establishing the details of this dependency.

SUMMARY

1. Ratios of vagility to vicariant spatial scale dictate ecological and biogeographical patterns.
2. The bulk of dispersal-speciation events occur within fairly well defined windows of interisland distance; within these windows, reciprocal dispersal and speciation events generate diversity rapidly.
3. Archipelagoes may provide similar sequences of such windows for quite disparate taxa at different times, thus nurturing the proliferation of taxa with different vagilities at different stages in the geological development of the archipelago. The resulting biogeographical patterns may be remarkably similar.
4. Extinction-prone taxa proliferate species, many of which become extinct; non-extinction-prone taxa generate a higher extant diversity.
5. Proneness to extinction has a limited influence on beta diversity.
6. High extinction rates continually update the relationship between the geological past and geographical distributions, eliminating the influence of "deep history" but deepening the imprint of contemporary history.
7. Chance has its greatest influence on taxa with very low and very high vagilities (i.e., low-diversity taxa); its effect is enhanced at extremes of extinction proneness.
8. The imprint of history on the biogeography of taxa is very predictable.
9. While alpha and gamma diversity may be quite unpredictable under some circumstances, their ratio (beta diversity) is generally very predictable.
10. Several measures of phylogenetic clade structure and development indicate that patterns within real clades are not likely to be adequately characterized by random structures or processes.