

Species-Area Relation and Self-Similarity in a Biogeographical Model of Speciation and Extinction

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We introduce a generic model for the population growth and dispersal of individuals in species with heterogeneous, fluctuating environments. New species originate with a probability inversely proportional to the abundance of the parent species. The model generates an average number of species which depends on the domain area in agreement with the species-area relation for islands. The model also generates self-similar radiations characterized by a power-law distribution for the number of subtaxa with the same parent taxon and a $1/f$ power spectrum for the time series of extinctions and originations. [S0031-9007(99)08604-4]

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Despite the complexity of factors which influence the population growth and dispersal of individuals in species, ecology and evolution exhibit several general patterns related to biogeography. In ecology, one example is the species-area relation where the number of species on islands (including continents) of similar climate and elevational range increases with the area of the island as a power law with an exponent of approximately 0.25: $S = CA^z$, where C is a constant and $z \approx 0.25$ [1–8]. A similar relationship, with exponent $z \approx 0.12$, holds for nested subareas within an island or continent. The species-area relation is observed for a wide range of fauna and flora including aquatic species in lakes of differing size. No generally accepted explanation of the species-area relation exists [5]. The relation may be a consequence of the canonical lognormal distribution [1,2] of the number of individuals in a species together with the assumption of a constant density of individuals [6]. However, the canonical lognormality of species-abundance curves is not well understood [7]. Two alternative qualitative theories of the species-area relation have been proposed: large areas have more species than small areas because (i) their greater range of distinct resources encourages ecological specialization [1–4] and (ii) large areas enjoy a lower extinction rate than small areas [8]. Neither theory is able to quantitatively predict the species-area relation.

In the fossil record, extinctions and originations of taxa often occur in episodic bursts such as adaptive radiations. One measure of the episodicity of extinctions and originations is the frequency distribution of the number of subtaxa within taxa. Burlando [9] computed this distribution for a variety of taxa and found that the frequency distribution, $f(n)$, is a power-law function with an exponent of -2 : $f(n) \propto n^{-2}$, where n is the number of subtaxa. His results suggest that a few lineages radiate copiously while most others radiate very little. There is also no characteristic number of subtaxa within taxa. Since rapidly radiating lineages also suffer high extinction rates [10], they produce

more subtaxa despite having, on average, shorter lifetimes than weakly radiating taxa. Thus, Burlando's [9] results can be taken as evidence for self-similar, episodic origination of taxa.

It has recently been reported that the power spectrum of time series of extinctions and originations of families in the fossil record is a power-law function of frequency, $S(f) = af^{-\beta}$, where a is a constant, f is frequency, and $\beta \approx 1$, for a variety of groups including both terrestrial and marine families [11]. This result, however, has been shown to be an artifact of the methodology [12]. It cannot be concluded, at present, what the time series statistics of extinctions and originations in the fossil record are because the fossil record does not present us with a time series at all. The fossil record data are the total number of extinctions and originations in a given stratigraphic interval. If stratigraphic intervals were all of the same duration, then the fossil record would represent a time series of extinction and origination rates. However, since stages are of widely varying duration, the fossil record is not a time series and no conclusions can be made at present about the time series statistics of extinctions and originations.

Hubbell [13] and Durrett and Levin [14] have produced stochastic computer models of biogeography with immigration, speciation, and extinction in a bounded domain in an attempt to quantitatively reproduce the species-area relation. The models of Hubbell [13] and Durrett and Levin [14] differ from the one presented in this paper in several important respects. In Hubbell's model [13] the dispersal rate is independent of abundance. In our model we will consider dispersal to be diffusive as often observed in spreading and invading species [15]. In the models of both Hubbell [13] and Durrett and Levin [14], the probability of speciation per unit area is independent of abundance. In our model we consider the speciation rate per unit area to be inversely proportional to the effective population size. This is consistent with the theory that most

speciation events are thought to occur primarily when population density is low (population “bottlenecks”) and rapid genetic drift drives evolutionary change [16].

A number of models have been presented which generate episodic bursts of extinctions and originations. Many of these models exhibit self-organized criticality (SOC). In SOC models of evolution, the extinction of one species (or higher taxa) can trigger the extinction of other species in a cascade through the food web [17,18]. New species subsequently fill the niches left by extinct species. Plotnick and McKinney [19] and Newman [20] have included the effects of environmental fluctuations to construct models of cascading extinctions. The drawback of these models is the lack of any biogeography. Speciation and extinction are both ultimately related to dynamic biogeography, the growth and dispersal of the number of individuals in a species. Extinction in nature occurs when the population of a species goes to zero. Speciation in nature occurs when a group of individuals reproductively isolated from other individuals in the parent species interbreed for a period of time long enough for the group to diverge from its parent population so that breeding with members of the parent species does not occur naturally [21]. Usually geographic isolation is responsible for the reproductive isolation. The isolation between founder population and parent population need not be complete [22].

In our model the population growth and dispersal is based on the classic equation of exponential growth with dispersal modeled by the diffusion equation [23]:

$$\frac{\partial n}{\partial t} = D\nabla^2 n + \eta(x, y, t)n, \quad (1)$$

where n is the local population density in a species, D is a constant, and $\eta(x, y, t)$ is a stochastic growth rate uncorrelated in space and time with a mean value of zero and a Gaussian distribution. We have modified the original equation of Skellam [23] and Kierstead and Slobodkin [24] by letting the growth rate be a random variable to model local variations in the population growth rate due to many complex factors such as stress induced by the physical environment including variations in climate, availability of nutrients or prey, and degree of predation by other species [25]. Diffusion is a classic model of dispersal that has been applied to both terrestrial and marine species [15]. In our model there is no explicit competition between species nor is there any explicit modeling of species fitness. Both of these factors may contribute, however, to the environmental heterogeneity in space and time that drives variability in abundances.

We have implemented (1) on an $L \times L$ lattice with an approximate discretization. We approximate (1) by assuming that the total abundance, N , is distributed throughout a circular range defined by its center and area, A . In our model each range area is incremented by an amount $cDN\Delta t$ in each time step where Δt is the duration of each time step and c is a constant, consistent with a diffusion

process. The population density of individuals in a species is not distributed uniformly within the range but is an uncorrelated random variable with variance $V \propto (N/A)^{3/2}$, where N/A is the mean population density. This relationship for the distribution of plants and animals within ranges is commonly observed [26–28] and is an extra assumption that goes into the model formulation. At each time step the population density at each grid point is multiplied by $\eta(x, y, t)$. Larger fluctuations in total abundance will result for species with smaller ranges because the standard deviation of the mean of m independent random variables decreases [29] as $m^{1/2}$. This is consistent with a decrease in abundance volatility [30] and extinction rate [31–33] for species with larger ranges observed in ecological and evolutionary data.

In our model, speciation occurs with each species and each grid point with a probability inversely proportional to the species abundance at that grid point. Speciation in nature is more likely to occur in small groups (population bottlenecks) since smaller populations exhibit faster genetic drift that facilitates peak shifts on the adaptive fitness landscape [16]. The exact functional dependence of evolutionary rate on population size depends on the specific structure of the adaptive fitness landscape, but simple, robust models suggest a dependence inversely proportional to effective population size [16].

When a new species originates in our model, it occupies one grid point chosen randomly within the range of its parent species and is given an abundance just above the threshold for extinction. Extinction occurs when the abundance falls below a threshold value at all grid points. Since extinction and speciation are both related to abundance (the former deterministically and the latter stochastically), they are observed in the model to be strongly correlated as observed in the fossil record [10]. Each simulation begins with a single species occupying a single grid point with an abundance just above the threshold for extinction.

Our model generates the species-area relation, a power-law distribution of the number of taxa with the same parent taxon, and $1/f$ noise extinctions and originations for a broad range of the free parameters D , the variance of $\eta(x, y, t)$, and the thresholds for extinction and speciation. To produce a species-area curve we have run the simulation for 10^5 time steps for lattice sizes $L \times L = 4, 16, 64, 256, 1024,$ and 4096 with all other constants kept the same. The average numbers of species for these different lattice sizes are presented as the bottom curve in Fig. 1. A straight line on a log-log plot with a slope of 0.25 is obtained, indicating that $S \propto A^{0.25}$, consistent with species-area relations often observed in the field. Similar results with $z \approx 0.25$ were obtained using a wide variety of free parameters, indicating that the result is quite robust. The curve corresponding to nested subareas within the island of size $L \times L = 4096$ is shown as the top curve in Fig. 1. This curve is given by $S \propto A^{0.13}$, also consistent with data. These results may be understood within the qualitative

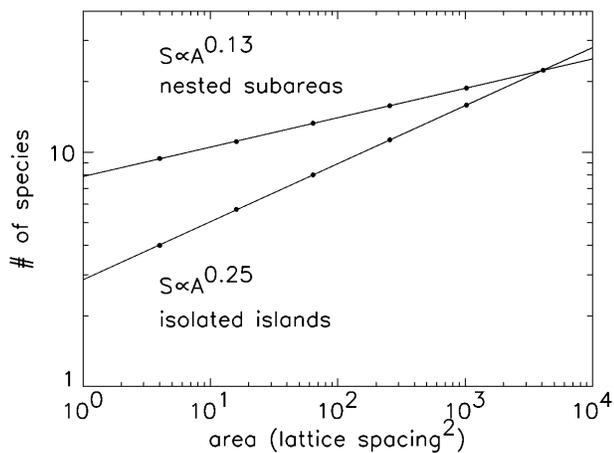


FIG. 1. Number of species, averaged over 10^5 time steps, as a function of simulation area for nested subareas (top) and isolated domains (bottom). The results indicate that $S \propto A^{0.25}$ for isolated islands and $S \propto A^{0.13}$ for nested subareas.

theory of MacArthur and Wilson [8]. MacArthur and Wilson hypothesized that extinction rates declined for increasing island area. This effect is also present in our model, since abundances fluctuate less when the range is large. Many species will be unaffected by this area dependence since the island may be larger than their range. However, those widespread species whose ranges fill the island are unable to take advantage of a lower extinction rate the way they could if they were on a bigger island and could extend their ranges. Decreased extinction rates result in more species for larger islands. This interpretation is consistent with the results of Schoener and Spiller [34] who found that the short-term survivability of introduced species of island spiders did not depend on island area (since none of the species had spread out to fill an island) but that the long-term survivability, limited by the size of each island, did.

The time series of extinction and origination with $L \times L = 4096$ are shown in Figs. 2a and 2b, respectively. The time series are strongly correlated and exhibit bursts of activity possibly analogous to mass extinctions and adaptive radiations. The skew of the time series can be varied by varying the parameters of the model, but a $1/f$ spectrum is obtained for nearly all finite values of the free parameters. The power spectrum of the time series is shown in Fig. 2c. The power spectra have a power-law dependence on frequency with $\beta = 1$: $S(f) \propto f^{-1}$. The generation of $1/f$ noise in this model is sensitive to the details of the model formulation. As a test, we assumed that individuals in a species were distributed uniformly within the species' range rather than taken from a random variable with variance $V \propto (N/A)^{3/2}$. The result was a model with self-affine behavior and a power-law species area relation but with exponents $\beta = 1.25$ and $z = 0.40$, respectively.

The cumulative frequency distribution of the number of subtaxa with the same parent taxon is presented in

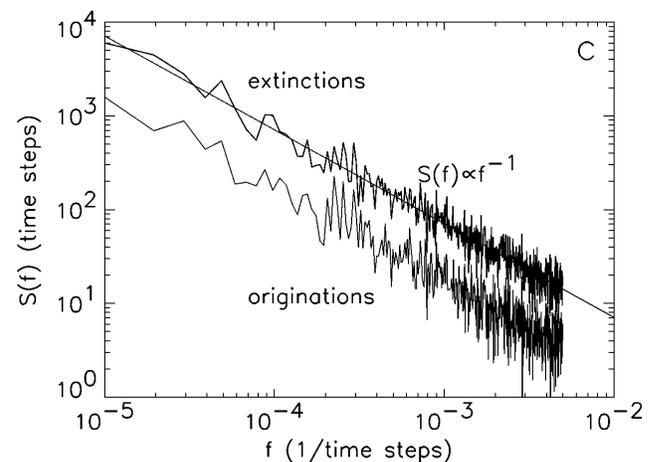
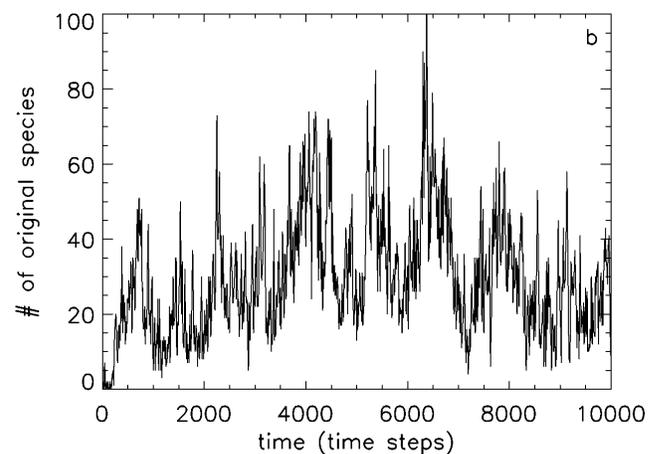
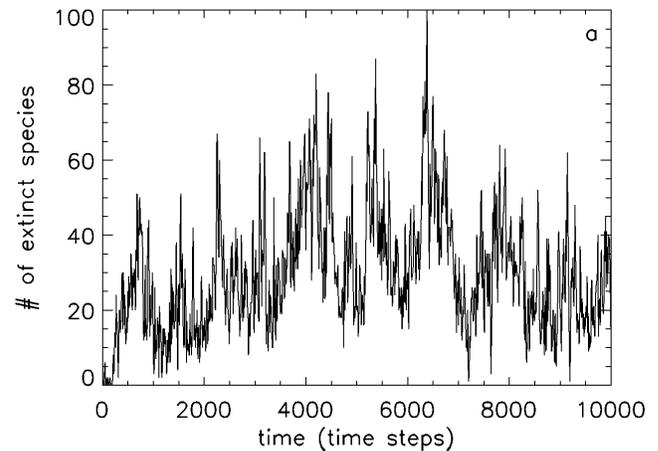


FIG. 2. (a) Number of species that become extinct during an interval of 100 time steps as a function of time step. Bursts of activity clustered in time with a wide range of extinction rates are observed. (b) Number of species that originate during an interval of ten time steps as a function of time step for the same simulation as for (a). (c) Power spectra of the time series of (a) and (b). Power-law power spectra with $S(f) \propto f^{-\beta}$ and $\beta = 1$ are obtained.

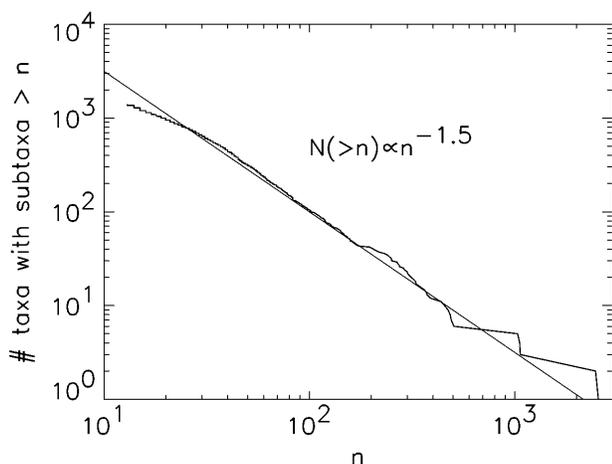


FIG. 3. Cumulative frequency distribution of taxa with at least n daughter taxa. A power-law distribution with an exponent of -1.5 is obtained.

Fig. 3. The plot indicates that the cumulative distribution is a power law with an exponent of -1.5 , indicating the self-similar radiation of lineages as observed in the fossil record by Burlando [9].

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- [1] F. W. Preston, *Ecology* **41**, 611–627 (1960).
- [2] F. W. Preston, *Ecology* **29**, 185–215 (1962).
- [3] E. F. Conner and E. D. McCoy, *Am. Nat.* **113**, 791–833 (1979).
- [4] M. L. Rosenzweig, *Species Diversity in Space and Time* (Cambridge University Press, New York, 1995).
- [5] I. Hanski and M. Gyllenberg, *Science* **275**, 397–400 (1997).
- [6] R. M. May, in *Ecology and Evolution of Natural Communities*, edited by M. L. Cody and J. M. Diamond (Belknap Press, Cambridge, MA, 1975), pp. 81–120.
- [7] G. Sugihara, *Am. Nat.* **116**, 770–787 (1980).
- [8] R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography* (Princeton University Press, Princeton, NJ, 1967).
- [9] B. Burlando, *J. Theor. Biol.* **163**, 161–172 (1993).
- [10] S. M. Stanley, *Macroevolution: Pattern and Process* (W. H. Freeman and Co., San Francisco, 1979).
- [11] R. V. Sole *et al.*, *Nature (London)* **388**, 764–767 (1997).
- [12] J. W. Kirchner and A. Weil, *Nature (London)* **395**, 337–338 (1998).
- [13] S. P. Hubbell, in *Preparing for Global Change: A Midwestern Perspective*, edited by G. R. Carmichael, G. E. Folk, and J. L. Schnoor (SPB Academic Publishing, Amsterdam, 1995), pp. 173–201.
- [14] R. Durrett and S. Levin, *J. Theor. Biol.* **179**, 119–127 (1996).
- [15] D. A. Andow *et al.*, *Landscape Ecology* **4**, 177–188 (1990).
- [16] N. H. Barton, in *Speciation and Its Consequences*, edited by D. Otte and J. A. Endler (Sinauer Associates, Inc., Sunderland, MA, 1989), pp. 229–256.
- [17] P. Bak and K. Sneppen, *Phys. Rev. Lett.* **71**, 4083 (1993).
- [18] K. Sneppen *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 5209–5214 (1995).
- [19] R. E. Plotnick and M. L. McKinney, *Palaos* **8**, 202–212 (1993).
- [20] M. E. J. Newman, *Proc. R. Soc. London B* **263**, 1605–1610 (1996).
- [21] E. Mayr, *Evolution* **36**, 1119–1132 (1982).
- [22] N. H. Barton and B. Charlesworth, *Annu. Rev. Ecol. Syst.* **15**, 133–164 (1984).
- [23] J. G. Skellam, *Biometrika* **38**, 196–218 (1951).
- [24] H. Kierstead and L. B. Slobodkin, *J. Mar. Res.* **12**, 141–147 (1953).
- [25] W. P. Sousa, *Annu. Rev. Ecol. Syst.* **15**, 353–391 (1984).
- [26] L. R. Taylor, *Nature (London)* **189**, 732–735 (1961).
- [27] L. R. Taylor and R. A. J. Taylor, *Nature (London)* **265**, 415–421 (1977).
- [28] R. M. Anderson *et al.*, *Nature (London)* **296**, 245–248 (1982).
- [29] A. M. Yaglom, *An Introduction to the Theory of Stationary Random Functions* (Prentice Hall, Englewood Cliffs, NJ, 1962).
- [30] D. S. Glazier, *Oikos* **47**, 309–314 (1986).
- [31] T. A. Hansen, *Paleobiology* **6**, 193–207 (1986).
- [32] S. M. Stanley, *Paleobiology* **12**, 89–110 (1986).
- [33] M. L. McKinney and D. Frederick, *Geology* **20**, 343–346 (1992).
- [34] T. W. Schoener and D. A. Spiller, *Science* **267**, 1811–1813 (1995).