



PSD
Z
(B)

Spatial Models for Species-Area Curves

RICK DURRETT† AND SIMON LEVIN‡

† *Cornell University, Department of Mathematics, Ithaca, NY 14853-7901 and*

‡ *Princeton University, Department of Ecology and Evolutionary Biology, Princeton, NJ 08544-1003, U.S.A.*

(Received on 16 February 1995, Accepted in revised form on 20 October 1995)

Inspired by earlier work of Hubbell, we introduce a simple spatial model to explain observed species-area curves. As in the theory of MacArthur and Wilson, our curves result from a balance between migration and extinction. Our model predicts that the wide range of slopes of species-area curves is due to the differences in the rates at which new species enter this system. However, two other predictions, that the slope increases with increasing migration/mutation and that the curves for remote islands are flatter than those for near islands, are at odds with some interpretations of data. This suggests either that the data have been misinterpreted, or that the model is not sufficient to explain them.

© 1996 Academic Press Limited

1. Introduction

One of the most profound and important empirical observations in ecology is that larger areas contain more species than smaller areas. For understanding how communities are organized or what the consequences of reserve design are for the maintenance of biodiversity, no relationship is more informative. Yet an understanding of what determines species-area curves remains elusive to this day.

Increasing areas can support more species both because the increasing habitat heterogeneity allows greater potential for specialization, and because even in a homogeneous environment smaller areas are to some extent random samples drawn from a larger population of species not all of the same size (Preston, 1962). The exact dependence of species number S on area A is debated (Johnson & Raven, 1973; Connor & Simberloff, 1978; Gilbert, 1980; McGuinness, 1984). Early studies (e.g. Hopkins, 1955) fitted the curve $S = a \ln(1 + bN)$, a relationship that would be expected if the individuals in a region were a random sample from a larger population (Preston, 1969). The most accepted relationship, however (Kilburn, 1966; MacArthur & Wilson, 1967; May,

1975; Connor & McCoy, 1979; Coleman, 1981; Sugihara, 1981), takes the logarithm of S to be proportional to log area, plus a constant; that is, S is proportional to a power of A .

Hubbell (to appear, 1995; see also Hubbell & Foster, 1986) has sought theoretical explanations of the observed species-area curves, extending ideas of MacArthur (1969) and Rosenzweig (1975) and incorporating dispersal and speciation. In this paper we build on Hubbell's work, addressing the last two of four questions posed by Williamson (1988) in a review of the concepts and empirical data on species-area relationships.

(3) Why is the power ρ in general between 0.15 and 0.4?

(4) Why is there so much variation in the power among surveys?

To help motivate these questions, we refer to Table 1, which gives the slopes for various data sets taken from MacArthur & Wilson (1967), Preston (1962), Johnson & Raven (1973), Connor & Simberloff (1978) and van der Werff (1983). In brief our answer to question (4) is: the power ρ is related to the rate (called α in our models below) at which new species enter the system. There is so much variation in the power α because the

TABLE 1
Some typical species-area curve powers z

| Fauna or Flora | Location | z |
|------------------|-----------------------|-------|
| Birds | Finland | 0.146 |
| Flora | Britain | 0.189 |
| Birds | Maryland | 0.213 |
| Land vertebrates | Lake Michigan Islands | 0.239 |
| Birds | East Indies | 0.280 |
| Mammals | East Indies | 0.280 |
| Ponerine ants | Melanesia | 0.300 |
| Amphibians | West Indies | 0.301 |
| Birds | East-Central Pacific | 0.303 |
| Land plants | Galapagos Islands | 0.325 |
| Carabid beetles | West Indies | 0.340 |
| Birds | Gulf of Guinea | 0.489 |

appropriate values of α may differ by several orders of magnitude.

2. Development of the Models

In the models that we consider space is divided into square cells. The centers of these are represented by the two-dimensional integer lattice, \mathbb{Z}^2 , the points in space with integer coordinates. We begin by describing Hubbell's model (to appear), in which time is discrete (i.e., $t = 0, 1, \dots$) and at any time t the state of each site is described by giving a list of the species found at that site. To make the transition from time t to time $t + 1$ we sequentially apply the following three processes to the entire grid.

(i) Speciation. At each site x , each species at x is replaced by a new species, also located at x , with probability α .

(ii) Dispersal. At each site x , and for each of the eight neighbors y that differ from x by at most one in either coordinate, each species at x can disperse onto y with probability b .

(iii) Competition. If at the end of step (ii) there are n species at a site, then each survives with probability $c/(1 + n)$.

The speciation, dispersal, and competition events for different species or for different sites are independent. This means that in the computer realization of the model they are determined by different calls to a random number generator.

Hubbell's model is somewhat complicated to program because each site must have a data structure that allows for the storage of a variable number of species. To avoid this problem we will adopt a finer spatial scale in which there can be at most one species per site. We index our species by points from the interval $(0, 1)$, so we can pick new species at random from the set of possibilities and not duplicate an existing species. Thus, at any time t , the state of

site x , $\xi_t(x)$, can be 0, indicating a vacant site, or a real number w with $0 < w < 1$, indicating that it is occupied by one individual of species w .

Our models take place in continuous time, i.e., t can be any non-negative real number, so they are formulated in terms of transition rates. We say something happens at rate λ if the probability of an occurrence between times t and $t + h$ is $\approx \lambda h$ when h is small. When things happen at a constant rate [like the death rates in (ii) below], the interoccurrence times t_i are independent and have an exponential distribution with mean $1/\lambda$, i.e. $P(t_i > t) = e^{-\lambda t}$.

To define our model, known in the mathematics literature as the "multitype contact process with mutation", we begin by introducing the dispersal kernel $p(x, y)$, which is the probability an offspring is sent from x to y . To have a spatially homogeneous model, we will assume p depends only on the distance between the two sites, i.e., $p(x, y) = p(|y - x|)$.

(i) At rate β an occupied site x produces an offspring of its type, and sends it to y with probability $p(x, y)$. If y is already occupied then no birth occurs. A mean number μ of propagules can be produced at rate β/μ without substantially changing the results we will state, but we will stick to the simpler formulation.

(ii) An occupied site becomes vacant at rate δ . This represents death of existing individuals.

(iii) An occupied site changes to a new type w' , chosen uniformly on $(0, 1)$, at rate α .

The changes referred to in (iii) have two possible interpretations: (a) the introduction of new species from outside the system by migration, or (b) genetic changes that introduce new species. We expect that the first mechanism will be more important for island groups, whereas the second may be more important for terrestrial situations such as the flora of Britain. Under either interpretation α will be very small; but, typically, the rates appropriate for (b) will be several orders of magnitude smaller than those for (a). It might be slightly more realistic to allow new types to appear in situation (a) at vacant sites or in (b) during the birth step. However, this will not make a significant difference in the behavior of the model except to change the effective value of α .

Turning to (i) and (ii), we note that if we ignore the types of the individuals then our model reduces to the "contact process", an interacting particle system that has been extensively studied for more than 20 years. For the mathematical theory see Harris (1974), Chapter VI in Liggett (1985), Chapters 4 and 11 in Durrett (1988), or Durrett (1991). For biological applications see Barkham & Hance (1982), Crawley & May 1987, Inghe (1989), or Durrett & Levin

max
num
of species?

(1994). The contact process (with or without mutation) obviously ignores many aspects of the growth and competition of plants. However, it is spatially explicit and captures what we believe are the essential features of the interaction—there is a limited carrying capacity and offspring are born near their parents.

In the above, we have made the assumption that the birth and death rates and displacement distribution do not depend on the species. It would be easy, within the contact-process framework, to allow for a spread of such rates. However, introduction of different rates for different species would introduce a Pandora's box of complications: stronger species will start to exclude weaker ones competitively; and, having admitted different types of individuals, we should logically allow succession to occur, i.e., some types can invade sites occupied by other types. Introducing such mechanisms in the name of realism would, in our opinion, result in an overly complicated model where one could not be sure what features of the model are responsible for the observed qualitative behavior. Instead we have taken a minimalist approach in constructing our model in order to answer the question: what would species-area curves look like in a homogeneous world where the only forces at work were migration or mutation, colonization, and extinction?

Before stating our first result we need to give some definitions and recall some "well-known" facts about the contact process. A "stationary distribution" for the contact process or multitype contact process with mutation is a possible equilibrium state. That is, if the initial state of the system, ξ_0 , has this distribution then the state at time t , ξ_t , has this distribution for all $t > 0$. Since the state of the system at any time t is an assignment of a number in $(0, 1)$ to each site $x \in \mathbb{Z}^2$, the distribution of the state is given by describing the joint distribution of $\xi_t(x_1), \dots, \xi_t(x_n)$ for all finite sets $\{x_1, \dots, x_n\} \subset \mathbb{Z}^2$. The (distribution of the) initial state is a stationary distribution if all these "finite dimensional distributions" are the same when computed at time t or at time 0. For further explanation, see Durrett & Levin (1994).

Either version of the contact process [i.e., with or without rule (iii)] has a trivial stationary distribution in which $\xi_t(x) = 0$ for all x and t . Clearly, increasing β makes it easier for the contact process to have a non-trivial stationary distribution; one that puts no mass on the all 0's state. Harris (1974) showed that for the basic contact process there is a critical value $\lambda_c > 1$, which depends on the dispersal function $\rho(z)$, so that for $\beta/\delta > \lambda_c$ the basic contact process has a

non-trivial stationary distribution. Bezuidenhout & Grimmett (1990) showed that there was only one non-trivial stationary distribution. By combining their result with an idea from Neuhauser (1992), one can show:

Lemma 1. Suppose $\beta/\delta > \lambda_c$. Then the contact process with mutation has a unique non-trivial stationary distribution, which we will denote by ξ_∞ . The importance of this result is simple. We want to study species-area curves for the contact process with mutation when it is in equilibrium, so we need to know that there is a unique equilibrium. Proofs of Lemma 1 and of the other results stated below can be found in the companion paper by Bramson *et al.*, (1996).

For a variety of reasons, we will also be interested in an even simpler version of the model above, called the "voter model with mutation," which evolves as follows:

- (i) A site x is always in some state $w \in (0, 1)$. At rate δ , it changes its state to that of a randomly chosen neighbor, picking y with probability $p(x, y) = \rho(|y - x|)$.
- (ii) At rate α , a site changes to a new type w' chosen uniformly on $(0, 1)$.

Again, we will use $\xi_t(x)$ to denote the state of site x at time t . The name "voter model" comes from thinking of the collection of sites, \mathbb{Z}^2 , as a rectangular grid of houses and $\xi_t(x)$ as the opinion of the voter at x at time t . Our voters are very simple-minded. Each voter keeps an opinion for an exponentially distributed amount of time with mean $1/\delta$ then adopts the opinion of a neighbor, with a voter at x picking neighbor y with probability $p(x, y)$. While one could argue that actual voters are equally naive, the point of studying the voter model is not to explain current political trends, but instead to gain insight into the behavior of the more complicated multitype contact process.

Mathematically, the voter model with mutation can be thought of as the multitype contact process with mutation with birth rate $\beta = \infty$. That is, when a death creates a vacant site at x , it is immediately filled in, with neighbor y having probability $p(x, y)$ to be the first to fill the site. One does not have to believe that β is enormous, however, to replace the contact process by the voter model. When $\beta = 10\delta$ in the contact process, approximately 90% of the sites are occupied in equilibrium. If one recalls that β represents the rate at which propagules are produced times the mean number produced, then ten does not seem to be an unreasonably large value.

$$\phi = \log N_r = \phi(r)$$

The voter model was first studied by Holley & Liggett (1975). More recently, it has appeared (slightly generalized) in the work of Silvertown *et al.* (1992) on the competitive interaction of grass species. The voter model is particularly simple to analyse because there is a "duality" that allows us to reduce questions about the voter model to questions about random walks. We will not go into the details here, but only mention that this duality is the key to the proofs of the results in the next section and is even useful in simulating the system efficiently. As in the case of the contact process, we need to know there is a unique stationary distribution before we can study the associated species-area curves, and this is true.

Lemma 2. The voter model with mutation has a unique stationary distribution, which we will denote by ξ_∞ .

3. Mathematical Results for Species-Area Curves

We would like to be able to prove results for the multitype contact process with mutation under the assumption that the dispersal function $p(x, y) = \rho(|y - x|)$ has finite variance, that is, $\sum_z |z|^2 \rho(z) < \infty$. However, for technical reasons, we are only able to prove results for the voter model with a nearest neighbor interaction, i.e., $p(x, y) = 1/4$ if $|y - x| = 1$. The work of Neuhauser (1992) suggests that Theorems 1–3 below are also true for the multitype contact process. In Section 4 we will give simulation results to support this conclusion.

To explain the formulation of our results, we begin by observing that since the rate at which new species enter the system is small, we investigate the limiting behavior of the species-area curves as α approaches 0. The reader should not confuse this with setting $\alpha = 0$, which results in a trivial model in which new species never appear. Instead, what our analysis will give us is a slope that depends on α and is an approximation that becomes more exact the smaller α becomes.

Key to our approximation, mentioned in the previous paragraph, is the identification of a length scale L , which depends on α , over which we expect to see interesting behavior. To compute L , note that if we follow the ancestry of a site backwards in time, then the time until we encounter a "mutation" has an exponential distribution with mean $1/\alpha$. The successive displacements of parents from offspring form a random walk, so the distance from an individual to its first ancestor who experienced a mutation will be of order $1/\sqrt{\alpha}$. This leads quite naturally to the introduction of the length scale $L = 1/\sqrt{\alpha}$. To relate L to real distance, recall that

sites are by definition one unit on a side and have a size comparable to the spacing between individuals.

In what follows we will take as our basic unit of area the square of side L , that is $S_r = (-L/2, L/2]^2$. We include the right endpoint but not the left to make the number of points exactly equal to L^{2r} whenever L is an integer. To define the species-area curve we let N_r be the number of different species in S_r in equilibrium, and then plot the log of N_r vs. the log of the area of S_r , i.e., $2r \log L$. Since $\log L \rightarrow \infty$, as $\alpha \rightarrow 0$, we rescale by dividing by $\log L$ and plot

$$\phi(r) = \log N_r / 2 \log L,$$

which is a function of the dimensionless log of area, r . We then have the following three results, which are proved in Bramson *et al.* (1996).

THEOREM 1 As $\alpha \rightarrow 0$

$$\frac{\log N_r}{2 \log L} \rightarrow \begin{cases} 0 & \text{if } r \leq 1 \\ r - 1 & \text{if } r \geq 1 \end{cases} \quad \text{in probability.}$$

Here $X \rightarrow a$ in probability means that $P(|X - a| > \epsilon) \rightarrow 0$ for any $\epsilon > 0$.

The observations in the paragraph above the theorem lead easily to the fact that states of sites separated by a large multiple of L are almost independent. So for length scales larger than L the number of species will be proportional to area and the limiting curve has slope 1 for $r \geq 1$. Roughly, Theorem 1 says that

$$\log N_r \approx 2(r - 1) \log L \quad \text{for large } L \text{ when } r \geq 1$$

Our next result sharpens this conclusion.

THEOREM 2 If $r \geq 1$ then $\alpha \rightarrow 0$ (and $L \rightarrow \infty$)

$$\frac{N_r}{L^{2(r-1)} (\log L)^2} \rightarrow \frac{2}{\pi} \quad \text{in probability}$$

Intuitively, this says that $N_r \approx (2/\pi)(\log L)^2$ when L is large, so as $L \rightarrow \infty$

$$\frac{\log N_r}{2 \log L} \approx \frac{2 \log \log L + \log(2/\pi)}{2 \log L} \rightarrow 0$$

Our final result shows that when $r < 1$ the number of species does not go to ∞ as L does.

THEOREM 3 If $r < 1$ then as $\alpha \rightarrow 0$ the expected number of types, EN_r , converges to a constant C_r .

This result, and its proof, complete the following picture of the equilibrium state. Locations that are separated by more than L are largely independent. On smaller scales, i.e., L' with $r < 1$, the landscape

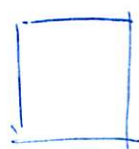
Basically
 $S \sim \alpha^{-1}$
 $S \rightarrow \text{const}$

$$\log N_r = \log \frac{2}{\pi} + 2(r-1) \log L + 2 \log \log L$$

L^r

$$\phi(r) \approx r$$

$$N_r \propto L^{2r}$$



right.

$$\frac{N_r}{L^{2r}} \rightarrow \frac{2}{\pi} (L) \quad ?$$

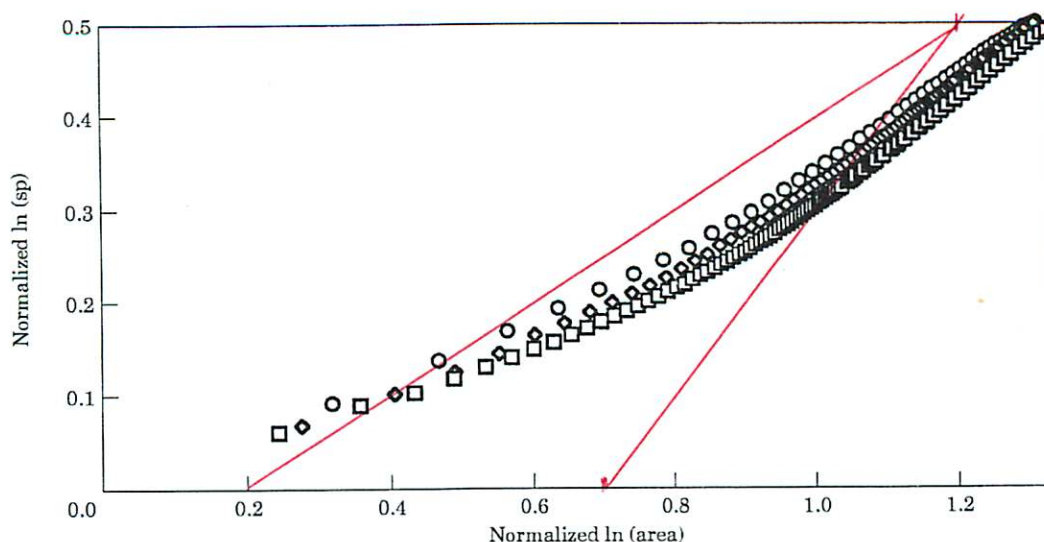


FIG. 1. Simulated species-area curves for the voter model with mutation. Here $L = 100, 200, 400$, $\alpha = 1/L^2$, and the universe is a $K \times K$ square where $K = L^{4/3}$. Notice that these curves are far from the limit, which is flat out to 1 and has slope 1 after that. \square , 400×400 ; \diamond , 200×200 ; \circ , 100×100 .

is relatively homogeneous, and has a positive probability (which depends on r) of being all one type.

4. Computer Simulations

In the discussions above we have asserted that (i) the multitype contact process with mutation and the voter model with mutation lead to similar species-area curves. A second point that will be important in the interpretation of these results below

is (ii) the species-area curve is almost linear for $0 \leq r \leq 1$. We have not been able to prove these results mathematically, so we will demonstrate them via computer simulation.

To deal with (i), Figs 1 and 2 give the results of simulations for the voter model with mutation and contact process with mutation on $(0, K)^2$ using nearest neighbor dispersal ($p(x, y) = 1/4$ if $|x - y| = 1$) and imposing periodic boundary conditions. That is, sites on the left edge of the square are neighbors of those on the right, those on the top edge are neighbors of

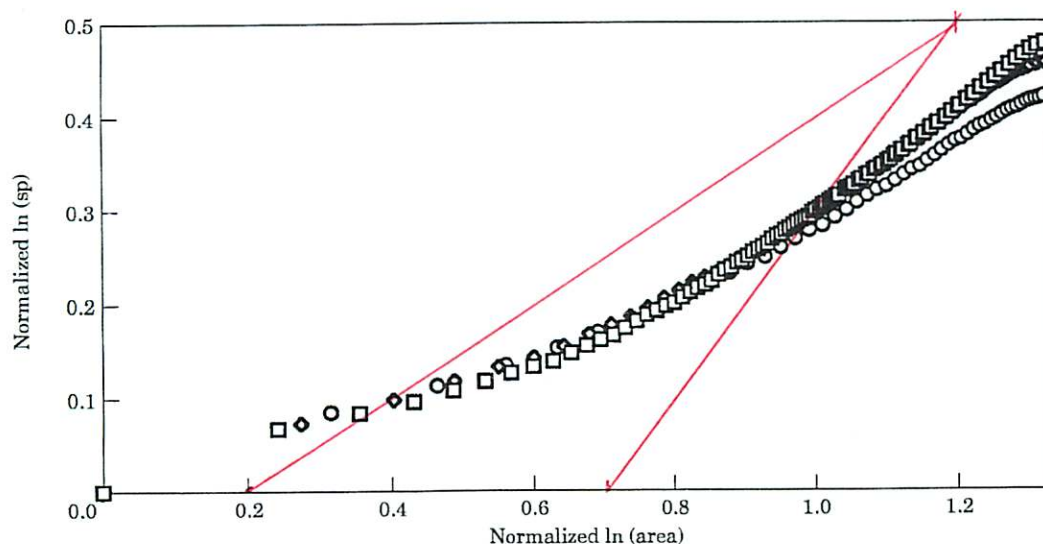


FIG. 2. Simulated species-area curves for the contact model with mutation. Here $L = 100, 200, 400$, $\alpha = 1/L^2$, and the universe is a $K \times K$ square where $K = L^{4/3}$. Notice that these curves are very similar to those for the voter model in Fig. 1. \square , 400×400 ; \diamond , 200×200 ; \circ , 100×100 .

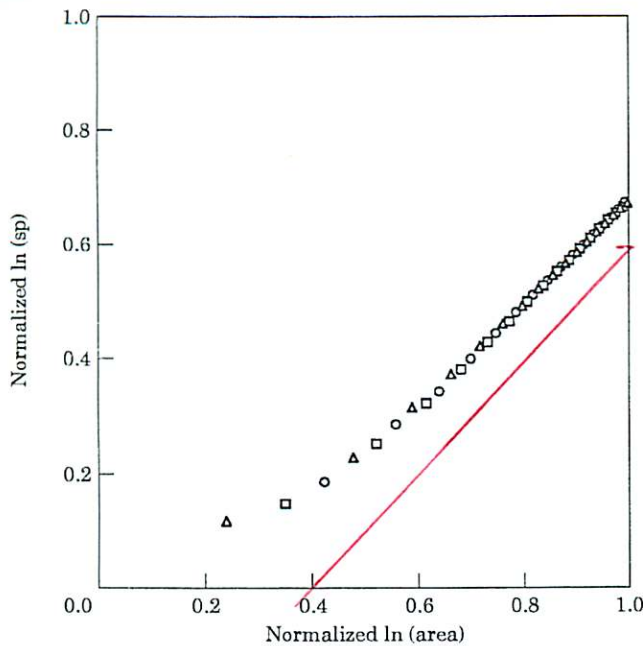


FIG. 3. Simulated species-area curves for toroidal (triangles), flat square (squares), and flat circular (circles) regions. Note that the three curves are almost identical showing that the species-area curve is not sensitive to the boundary conditions used.

those on the right; or in the description our computer prefers, the neighbors of a point are $\{y: |x - y| = 1\}$ where the difference $x - y$ is computed modulo K [e.g. $(0, 7) - (K - 1, 7) = (1, 0)$]. Periodic boundary conditions make our universe into a torus (or doughnut) but they eliminate boundaries and give us a universe that looks the same from every point it.

The main advantage for this is that on one simulation we can compute the species-area curves from a number of different centers (we use 100) and average the results to reduce the variance.

However, islands are not doughnuts floating on the ocean, and it is important to ask if the results are sensitive to the choice of boundary conditions. To investigate this point we have simulated the process on a square flat island and a round flat island. In the flat island simulations there is an array of habitable sites (land) surrounded by a boundary of uninhabitable ones (ocean) that can never become occupied. Figure 3 gives the average of ten simulations for flat (square), round (circle), and toroidal (triangle) islands with 10000 sites. The curves are so close that the graph is a mess when all three curves are plotted simultaneously. Thus, we have chosen to alternate plotting points from the three data sets.

Returning to the details of the simulation, we should also point out that when we are thinking about nested boxes within a land mass as in the example of the flora of the British Isles, K is a spatial cutoff, with no fixed relationship to the model parameters $L = 1/\sqrt{\alpha}$. In our first set of simulations we have taken $K = L^{4/3}$. Theorem 1 implies that in the limit as $K \rightarrow \infty$ the species-area curve will be flat out to 1 and then have slope 1. The realizations in Fig. 1 show that in the voter model we are far from this limit when $K = 400$ and there has not been much change from the curves from $K = 100$ and $K = 200$. Figure 2 shows three analogous results for the contact process. While we do not expect the curves to be identical for the two models, they are clearly very similar.

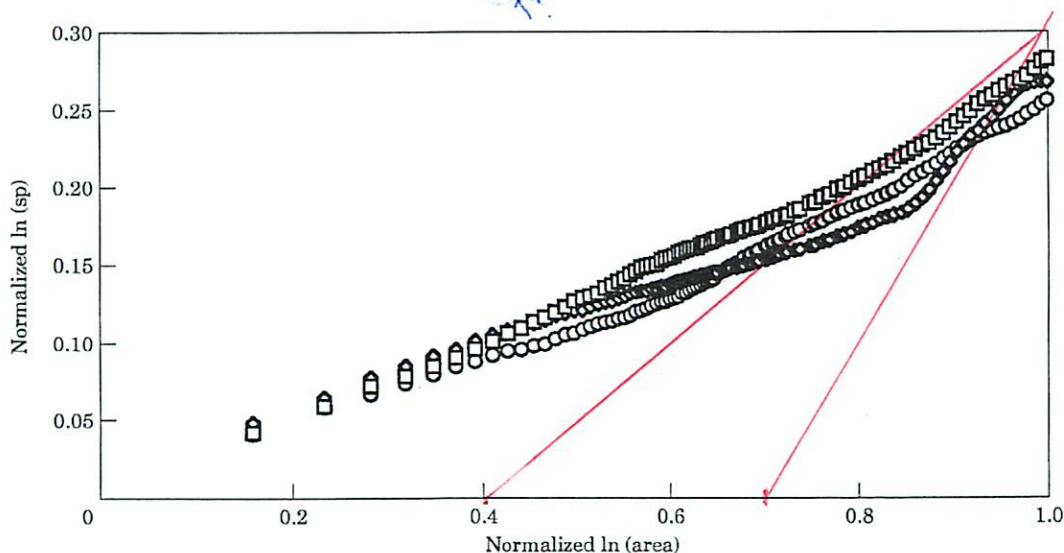


FIG. 4. Three simulated species-area curves for the voter model with mutation when $L = 1000$, $\alpha = 1/L^2 = 10^{-6}$. Note that the curves are fairly close to straight lines and there is little variation between runs.

To investigate the shape of the species-area curves for our models, we simulated the equilibrium distribution when $\alpha = 10^{-6}$ and hence $L = 10^3$. Since we were only interested in the behavior for $0 \leq r \leq 1$ we took $K = 10^3$. The results of three simulations graphed in Fig. 4 show that the curve is fairly straight and there is not too much variation among simulation runs.

5. Interpretation of our results

The first point to be made is that although the limiting curve in Theorem 1 consists of two straight lines with slopes 0 and 1, Theorem 2 allows us to compute a slope for species-area curves that depends on α . To calculate that slope, note that (i) the simulations discussed above suggest that the species-area curve is linear on log-log paper for $0 \leq r \leq 1$, (ii) Theorem 2 says $N_1 \approx (2/\pi)(\log L)^2$, and (iii) the number of species in a 1×1 box in the voter model with mutation model is always one, so $N_0 = 1$. Combining (i-iii) the slope of our species-area curve will be

$$\frac{\log N_1 - \log N_0}{2 \log L} \approx \frac{2 \log \log L + \log(2/\pi)}{2 \log L} \quad (1)$$

Plugging in different values of α we find the following slopes

| | | | | |
|----------|-----------|-----------|-----------|-----------|
| α | 10^{-4} | 10^{-5} | 10^{-6} | 10^{-7} |
| slope | 0.306 | 0.284 | 0.264 | 0.245 |

By varying $L = 1/\sqrt{\alpha}$ in (1) we can match the slopes in Table 1 from the flora of Britain to the birds of the East Central Pacific. Larger slopes, such as the birds of Guinea, can be obtained by using longer range migration (beyond nearest neighbors) in which case the $2/\pi$ in Theorem 2 will be replaced by a larger constant C that will depend on the dispersal distance.

Even though we can match the slopes in Table 1, the simple spatial models we are using are not designed to make quantitative fits, but instead to offer explanations for observed qualitative behavior. Thus, to answer Williamson's fourth question: our model predicts that there is so much variation among surveys because the rate α at which new species enter the system varies considerably.

The last observation is consistent with the view, see e.g. Preston (1962), that species-area curves are steeper for islands than for nested areas within a continent, since new species will arrive at a lower rate in the second case. Taking this reasoning one step further our formula predicts that the slope of

species-area curves for distant islands (with smaller α 's) should be flatter. This conclusion differs from much current theory (see e.g., the popular textbook by Begon *et al.*, 1990) that slopes are steeper for more distant island groups. However, data on this point are equivocal, and others have asserted that the opposite is true (Hamilton & Armstrong, 1965; Schoener, 1976; Connor & McCoy, 1979, p. 806; Williamson, 1981, p. 65; Williamson, 1988, p. 111).

A second widely accepted qualitative property of species-area curves that is in conflict with the predictions of our model is that higher mobility leads to smaller slopes. A commonly cited source for this conclusion is Wright (1981). However, inspection of his table on p. 737 reveals that apart from the data on the West Indies most "z-statistics" are barely above the 1.64 (standard deviations) needed for 95% confidence. For example, in the column comparing birds and non-volant mammals the values are 9.36 (West Indies), 2.5, 2.38, 2.02, 1.76, 0.78, 0.17, -0.08, -0.32 i.e., the result is significant in six cases out of ten.

Even if one accepts that birds have significantly smaller slopes, this does not automatically falsify the model. One can argue that (i) birds move easily from one island to another, and (ii) it is the availability of suitable habitat that determines if they settle, so the slopes of their species-area curves are determined by

| | | | | |
|-----------|-----------|------------|------------|------------|
| 10^{-8} | 10^{-9} | 10^{-10} | 10^{-11} | 10^{-12} |
| 0.229 | 0.215 | 0.202 | 0.191 | 0.182 |

those of the relevant vegetation. Clearly the points in the last three paragraphs bear closer examination.

One possible source of error in our analysis is that we equate the slope of the species-area curve $\phi(r)$ with that of the difference $\phi(1) - \phi(0)$. Since islands of a fixed size will have fewer species in more distant island groups, the associated species-area curves can be steeper only if they reach 0 (i.e., one species) at a higher level.

Finally, in applying our model to island groups we have certainly made a gross simplification by supposing that new species arise on each island at a constant rate per square meter. Certainly smaller islands will receive new species from larger ones nearby, while new species can enter the island group only by being dispersed very long distances. This makes it clear that our simple picture ignores important details. However, to model an entire island group directly would lead to a model that is both hopelessly complicated and specific to a given island group.

6. Conclusions

The considerations of this paper show that many of the properties of species-area curves can be explained in general terms with one of the simplest interacting particle models. Our work is in the spirit of MacArthur & Wilson's (1963, 1967) theory in that the number of species is a result of a dynamic equilibrium between immigration and extinction. However, in contrast to MacArthur & Wilson, who use two unspecified monotone functions to describe immigration and extinction (see fig. 4, p. 376 in their 1963 paper or the same figure on p. 22 of their 1967 book), our model has precisely specified dynamics that enable us to make quantitative as well as qualitative predictions.

Our most important prediction is that the slope z of the species-area curve on log-log paper depends on the rate α at which new species enter the system. This is in contrast to earlier work of for example Preston (1962) and May (1975) who predicted a unique value of $z \approx 1/4$, and seems to be in better agreement with the data quoted in Table 1 which shows a wide variety of slopes. In particular this allows us to see that the "areas within continents" and "island groups" situations are not really different but simply correspond to quite different values of the rate α .

The predictions above must be compared with the existing data. Given the controversy that has surrounded explanations of species-area curves (see e.g., Connor & McCoy, 1979; Gilbert, 1980; McGuinness, 1984) it would be foolish to claim that our new variation of the equilibrium theory of MacArthur & Wilson suddenly solves a century-old problem. At the very least, it is clear that habitat diversity, which is ignored in our model, plays an important role in some situations. However, we feel that our approach through spatial models sheds some new light on an old puzzle. Certainly it will generate some new heat as well.

We would like to thank Steve Hubbell for sharing his ideas with us, and Linda Buttel for performing the simulations and making the graphs in Figs 1-4. We are grateful to referees Alan Hastings and Michael Rosenweig for suggestions and criticisms that inspired us to improve this paper. Durrett was partially supported by the National Science Foundation and by the Army Research Office through the Mathematical Sciences Institute at Cornell University. Levin is pleased to acknowledge the support of the Department of Energy through grant DE-FG02-94ER 61815 and the National Aeronautics and Space Administration through grants NAGW-3124 and NAGW-3741 to Princeton University.

REFERENCES

- BARKHAM, J. P. & HANCE, C. E. (1982). Population dynamics of the wild daffodil (*Narcissus pseudonarcissus*) II. Implications of a computer model of 1000 years of population change. *J. Ecol.* **70**, 323-344.
- BEGON, M., HARPER, J. L. & TOWNSEND, C. R. (1990). *Ecology: Individuals, Populations and Communities*. 2nd edn. Boston MA: Blackwell Scientific Publications.
- BEZUIDENHOUT, C. & GRIMMETT, G. (1990). The critical contact process dies out. *Ann. Probab.* **18**, 1462-1482.
- BRAMSON, M., COX, J. T. & DURRETT, R. (1996). Spatial models for species area curves. In preparation.
- COLEMAN, B. D. (1981). On random placement and species area relations. *Math. Biosci.* **54**, 191-215.
- CONNOR, E. F. & MCCOY, E. D. (1979). The statistics and biology of the species area relationship. *Am. Nat.* **113**, 791-833.
- CONNOR, E. F. & SIMBERLOFF, D. (1978). Species number and compositional similarity of the Galapagos flora and avifauna. *Ecol. Monogr.* **48**, 219-248.
- CRAWLEY, M. J. & MAY, R. M. (1987). Population dynamics and plant community structure: competition between annuals and perennials. *J. theor. Biol.* **125**, 475-489.
- DURRETT, R. (1988). *Lecture Notes on Particle Systems and Percolation*. Belmont CA: Wadsworth Publishing Company.
- DURRETT, R. (1991). The contact process: 1974-1989. In: *Mathematics of Random Media* (Kohler, W. E. & White, B. S. eds) pp. 1-18. Providence RI: American Mathematical Society.
- DURRETT, R. & LEVIN, S. A. (1994). Stochastic spatial models: a user's guide to ecological applications. *Phil. Trans. Roy. Soc. B*, **343**, 329-350.
- GILBERT, F. S. (1980). The equilibrium theory of biogeography: fact or fiction. *J. of Biogeography* **7**, 209-235.
- HAMILTON, T. H. & ARMSTRONG, N. E. (1965). Environmental determination of insular variation in bird species abundance in the Gulf of Guinea. *Nature* **207**, 148-151.
- HARRIS, T. E. (1974). Contact interactions on a lattice. *Ann. Probab.* **4**, 175-194.
- HOLLEY, R. A. & LIGGETT, T. M. (1975). Ergodic theorems for weakly interacting systems and the voter model. *Ann. Probab.* **3**, 643-663.
- HOPKINS, B. (1955). The species area relations of plant communities. *J. Ecol.* **43**, 409-426.
- HUBBELL, S. P. & FOSTER, R. B. (1986). Biology, chance, history, and the structure of tropical rain forest tree communities. In: *Community Ecology* (Diamond, J. M. & Case, T. J., eds) pp. 314-330. New York: Harper and Row.
- HUBBELL, S. P. (1995). Towards a theory of biodiversity and biogeography on continuous landscapes. In: *Preparing for Global Change: A Midwestern Perspective* (Carmichael, G. R., Folk, G. E. & Schnoor, J. L., eds) pp. 173-201. Amsterdam: SPB Academic Publishing.
- HUBBELL, S. P. (to appear). *A Theory of Biogeography and Relative Species Abundance*. Princeton NJ: Princeton University Press.
- INGHE, O. (1989). Genet and ramet survivorship under different mortality regimes—a cellular automaton model. *J. theor. Biol.* **138**, 257-270.
- JOHNSON, M. P. & RAVEN, P. H. (1973). Species number and endemism: The Galapagos archipelago revisited. *Science* **179**, 893-895.
- KILBURN, P. D. (1966). Analysis of the species area relation. *Ecology* **47**, 831-843.
- LIGGETT, T. M. (1985). *Interacting Particle Systems*. New York: Springer-Verlag.
- MACARTHUR, R. H. (1969). Patterns of communities in the tropics. *Biol. J. Linn. Soc.* **1**, 19-30.
- MACARTHUR, R. H. & WILSON, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution* **17**, 373-387.
- MACARTHUR, R. H. & WILSON, E. O. (1967). *The Theory of Island Biogeography*. Princeton Monographs in Population Biology. Princeton NJ: Princeton University Press.

- MAY, R. M. (1975). Patterns of species abundance and diversity. In: *Ecology and Evolution of Communities* (Cody, M. L. & Diamond, J. M. eds) pp. 81–120. Cambridge MA: Harvard University Press.
- MCGUINNESS, K. A. (1984). Equations and explanations in the study of species-area curves. *Biol. Rev.* **59**, 423–440.
- NEUHAUSER, C. (1992). Ergodic theorems for the multitype contact process. *Prob. Theor. Rel. Fields* **91**, 467–506.
- PRESTON, E. C. (1969). *An Introduction to Mathematical Ecology*. New York: Wiley.
- PRESTON, F. W. (1962). The canonical distribution of commonness and rarity. *Ecology* **43**, I. 185–215, II. 410–432.
- ROSENZWEIG, M. L. (1975). On continental steady states of species diversity. In: *Ecology and Evolution of Communities* (Cody, M. L. & Diamond, J. M. eds) pp. 121–141. Cambridge MA: Harvard University Press.
- SCHOENER, T. W. (1976). The species-area relationship within archipelagos: models and evidence from island land birds. In: *Proceedings of the 16th International Ornithological Conference* (Firth, H. J. & Calaby, J. H., eds) pp. 629–642. Canberra: Australian Academy of Science.
- SILVERTOWN, J., HOLTIER, S., JOHNSON, J. & DALE, P. (1992). Cellular automaton models of interspecific competition for space—the effect of pattern on process. *J. Ecol.* **80**, 527–534.
- SUGIHARA, G. (1981). $S = CA^z \approx 1/4$. A reply to Connor and McCoy. *Am. Nat.* **117**, 790–793.
- VAN DER WERFF, H. (1983). Species number, area and habitat diversity in the Galapagos Islands. *Vegetatio* **54**, 167–175.
- WILLIAMSON, M. (1981). *Island Populations*. Oxford: Oxford University Press.
- WILLIAMSON, M. (1988). Relationship of species number to area, distance and other variables. In: *Analytical Biogeography* (Myers, A. A. & Giller, P. S., eds) Chapter 4. London: Chapman and Hall.
- WRIGHT, S. J. (1981). Intra-archipelago vertebrate distributions: the slope of the species-area relation. *Am. Nat.* **118**, 726–748.