Local and Regional Regulation of Species-Area Relations: A Patch-Occupancy Model

Hal Caswell and Joel E. Cohen

Local species diversity (i.e., diversity in a small homogeneous patch of habitat) may be determined by local processes such as competition, predation, mutualism, and disturbance, or by regional processes such as speciation and biogeographical dispersal (Ricklefs 1987). Most recent ecological theory has focused on the local processes that determine membership in a community, rather than the regional processes that determine the species pool from which members may be drawn. One approach to distinguishing local from regional control of diversity is to examine a number of communities and plot local diversity as a function of the regional species pool (Terborgh and Faaborg 1980; Cornell 1985a, 1985b; Ricklefs 1987). In saturated communities local diversity should be independent of regional diversity. A direct relation between local and regional diversity, however, is interpreted as evidence that "in these cases, local communities are not saturated, diversity is not prescribed by local conditions, and the number of species found within small areas is sensitive to such regional processes as geographic dispersal . . ." (Ricklefs 1987, 168). The results of such tests have been mixed. Local diversity of cynipine wasps on oak trees (Cornell 1985a, 1985b) and songbirds on Caribbean islands (Ricklefs 1987) is more or less linearly correlated with regional diversity, thus providing no evidence of saturation of local communities. In another study of island birds in the Caribbean, however, Terborgh and Faaborg (1980) found that local diversity was independent of regional diversity above some minimum number of species.

In this chapter we construct a model that includes both local processes and a regional species pool, and which makes predictions about local diversity. We find that local-regional diversity regressions must be interpreted with care, because the interaction of disturbance, colonization, and competition in locally saturated communities can produce patterns that completely obscure the effects of saturation.

Any model intended to study local and regional regulation of species diversity must contain at least two spatial scales. Most of the classic theories of diversity, however, are based on species-interaction models (the Lotka-Volterra equations and their relatives) which include only a single scale. They focus on local processes to the exclusion of regional effects.

Patch-occupancy models, which include two spatial scales, are a next step in complexity and realism. They picture the world as a set of patches in which local species interactions take place. The state of a patch is defined by species presence or absence. If the collection of patches is well mixed, so that each patch interacts equally with all others, the system can be described by a set of differential or difference equations in the *proportions* of patches in each state. This assumption of mixing limits the scales to two: the local scale within a single patch and the regional scale of the entire set of patches. Patch-occupancy models were introduced by Cohen (1970) and Levins (1970), and have since been applied to a variety of ecological interactions (Slatkin 1974; Hastings 1977, 1978; Caswell 1978; Crowley 1979; Hanski 1983; Caswell and Cohen 1991a, 1991b).

Caswell and Cohen (1991b) used patch-occupancy models to examine coexistence and diversity in competitive and predator-prey interactions. In those models, coexistence is determined by the interplay of the rate of approach to local equilibrium (competitive exclusion) and the rates of disturbance and dispersal. Disturbance can maintain nonequilibrium coexistence and increase both alpha and beta diversity (Caswell and Cohen 1991b).

It is difficult to analyze patch-occupancy models with large numbers of species because the number of possible patch states increases exponentially with the number of species. Thus patch-occupancy models have been used primarily to describe two- and three-species interactions. Conclusions about species diversity rest on the usual ecological inference that diversity is determined by the outcome of such interactions. In this chapter, we develop a patch-occupancy model for large numbers of species, and examine the relation between local diversity and the regional species pool.

THE MODEL FRAMEWORK

We approximate the world by an effectively infinite set of effectively identical patches. This boring landscape is home to S_{tot} species. Each patch is independently subject to disturbance, with probability p, at each time step. A disturbance eliminates all species from a patch. The probability that species i will colonize a suitable patch is a species-specific constant c_i. By assuming that the c_i are constant, we ignore both neighborhood effects (which would make colonization probability depend on the prox-

imity of occupied patches; see Caswell and Etter 1993) and frequency effects (which would make colonization probability depend on the abundance of the species). Which patches are available for colonization, and what happens to the species once they have arrived, depend on the hypotheses made about local interaction.

We want to describe the patterns of diversity resulting from this simple model. To do so, we focus not on a single index but on the species-area curve. This curve gives not only the expected species richness in a single patch (the most local kind of diversity admitted in the model) but also the expected richness in two, three, . . . randomly selected patches. The slope of the species-area curve is one measure of beta diversity. Species-area curves are frequently reported, and there is a large literature on the functions suitable to describe them (McGuinness 1984a).

We will present two models, which differ in their assumptions about local processes. The first contains no competition of any kind. Communities in this model are never saturated, and there is no local limitation on either coexistence or diversity. The number of species in a patch depends only on the history of colonization since the most recent disturbance. At the other extreme, we model strong local saturation by supposing that there is one species that eventually excludes all the others from any patch that it colonizes.

Based on our experience with patch-occupancy models for several species (Caswell and Cohen 1991a, 1991b), we expect the time scales of disturbance and competition to play important roles in these models. If disturbance is frequent and competitive exclusion is slow, we expect the model with strong local saturation to behave like the noncompetitive model, because only rarely will a patch be undisturbed long enough for exclusion to occur. On the other hand, if disturbance is rare or exclusion is rapid, we expect local diversity to reflect competition, and local communities to be saturated with species.

NONCOMPETITIVE COMMUNITIES

A Single Patch

We begin with a single patch, without competition. Let c_i be the probability of species i arriving, per unit time, independently of all other species. Let p denote the probability of disturbance and t the time since the last disturbance ($t = 0$ means the patch is currently disturbed). We assume $p > 0$. Then the probability of finding species i in the patch is

(9.1) $P[\text{sp. } i \text{ present now}|t] = 1 - (1 - c_i)^t$

Let S denote the number of species in the patch. Since species colonize independently,

(9.2) $$E[S|t] = \sum_{i=1}^{S_{tot}} [1 - (1 - c_i)^t]$$

and thus

(9.3) $$E[S] = \sum_{t=0}^{\infty} E[S|t] P(t)$$
$$= \sum_{t=0}^{\infty} E[S|t] p(1 - p)^t$$

To proceed, we ignore variation in the colonization rate, setting $c_i = c$ for all i. Then, combining equations 9.2 and 9.3, we get

(9.4) $$E[S] = S_{tot} \left[1 - \frac{p}{p + c - pc} \right]$$

Thus, in this simple single-patch model, local diversity is directly proportional to the size of the regional species pool.

Species-Area Relationships

We turn now from single patches to collections of patches. We want to derive a species-area relation. Our approach is to calculate the expected species richness of a set of k patches, conditional on its disturbance history, and then take an expectation of this quantity over the probability distribution of disturbance histories.

Consider a random sample of k patches. We want to calculate the "age" distribution of this set of patches, where age is measured since the most recent disturbance. Let $D(t_1, t_2, \ldots, t_k)$ denote the event that patch j was last disturbed at time $-t_j$, for $j = 1, \ldots, k$. Because patches are disturbed independently with a common disturbance probability p, we know that

(9.5) $$P[D(t_1, \ldots, t_k)] = \prod_{j=1}^{k} p(1 - p)^{t_j}.$$

Consider species i. The conditional probability that species i is present in at least one of the k patches is

$P[\text{sp. } i \text{ present in some patch}|D(t_1, \ldots, t_k)] =$
$1 - P[\text{sp. } i \text{ absent from every patch}|D(t_1, \ldots, t_k)] =$
$$1 - \prod_{j=1}^{k} (1 - c_i)^{t_j} = 1 - (1 - c_i)^T$$

where $T = t_1 + \cdots + t_k$.

From this we can calculate the conditional expectation of the species richness in the collection of k patches

(9.6) $$E[S(k)|D(t_1 \ldots, t_k)] = \sum_{i=1}^{S_{tot}} [1 - (1 - c_i)^T]$$

so that the species-area relationship is given by

$$E[S(k)] = \sum_{t_1=0}^{\infty} \cdots \sum_{t_k=0}^{\infty} E[S(k)|D(t_1, \ldots, t_k)]$$

(9.7) $$\times \prod_{j=1}^{k} p(1 - p)^{t_j}$$
$$= \sum_{t_1=0}^{\infty} \cdots \sum_{t_k=0}^{\infty} \sum_{i=1}^{S_{tot}} \left[1 - (1 - c_i)^T \right] p^k (1 - p)^T$$

This expression can be simplified, because we can collect all those terms in which $t_1 + \cdots + t_k = T$, with $T \geq t_j \geq 0, j = 1, \ldots, k$, and write

(9.8) $$E[S(k)] = \sum_{T=0}^{\infty} H(T,k) \sum_{i=1}^{S_{tot}} \left[1 - (1 - c_i)^T \right] \cdot$$
$$\times p^k (1 - p)^T$$

where

(9.9) $$H(T,k) = \underbrace{\sum_{t_1=0}^{\infty} \cdots \sum_{t_k=0}^{\infty}}_{t_1 + \ldots + t_k = T} 1$$

$$(9.10) \qquad = \binom{T + k - 1}{k - 1}$$

Thus

$$(9.11) \quad E[S(k)] = \sum_{T=0}^{\infty} p^k (1 - p)^T \sum_{i=1}^{S_{tot}} [1 - (1 - c_i)^T]$$
$$\times \binom{T + k - 1}{k - 1}$$

If, as before, we simplify this by assuming that $c_i = c$ for all i, we obtain

$$(9.12) \quad E[S(k)] = p^k S_{tot} \sum_{T=0}^{\infty} (1 - p)^T [1 - (1 - c)^T]$$
$$\times \binom{T + k - 1}{k - 1}$$

Now for some combinatorial sleight-of-hand. We note that

$$(9.13) \qquad \binom{T + k - 1}{k - 1} = \binom{k + T - 1}{T}$$

and that these are the *figurate numbers* (Riordan 1958, 25). For any $r < 1$, these numbers satisfy

$$(9.14) \qquad \sum_{T=0}^{\infty} \binom{k + T - 1}{T} r^T = \frac{1}{(1 - r)^k}$$

(Riordan 1958, 10). Substituting this into equation 9.12 and simplifying, we obtain a final simplified expression for the species-area curve as a function of colonization, disturbance, and the species pool:

$$(9.15) \qquad E[S(k)] = S_{tot} \left[1 - \frac{p^k}{(p + c - pc)^k} \right]$$

Results for Noncompetitive Communities

Species-Area Relationships. The species-area curves produced by equation 9.15 look surprisingly realistic (fig. 9.1). They are nearly linear on a log-log scale for small k, eventually reaching an asymptote at S_{tot} as $k \to \infty$. Log-log species-area curves, of course, are a familiar sight in ecology, and have been interpreted in terms of competitive equilibrium, island biogeography theory, and the canonical lognormal distribution of species abundances (May 1975a; McGuinness 1984a). In particular, the canonical lognormal predicts a slope of 0.25, while reasonable but noncanonical lognormal distributions yield slopes between about 0.15 and 0.4 (May 1975a).

In our model, the slope and intercept of the species-area curve are largely determined by the ratio of the disturbance rate p and the colonization rate c. Figure 9.2A shows the intercept (i.e., $E[S(1)]$) as a function of p/c. There is a sharp threshold in the neighborhood of $p/c = 1$; when $p/c \gg 1$, an individual patch tends to contain only a fraction of the species pool ($E[S(1)] \ll S_{tot}$). When $p/c \ll 1$, each patch is expected to contain most of the available species and $E[S(1)] \approx S_{tot}$. This threshold can be shown analytically by rewriting equation 9.15 as
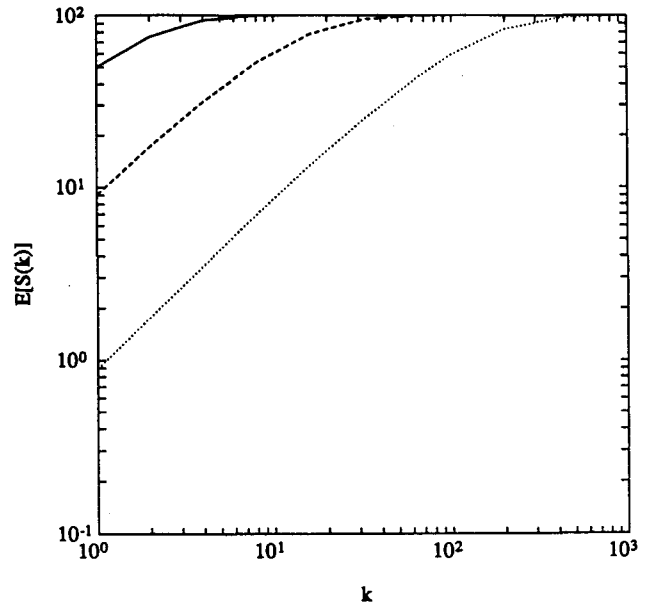

Figure 9.1   Species-area curves for the noncompetitive model. $c = .001$ and $S_{tot} = 100$ throughout. Solid line, $p = .001$; dashed line, $p = .01$; dotted line, $p = .1$.

$$(9.16) \qquad E[S(1)] = S_{tot} \left(\frac{1 - p}{p/c + 1 - p} \right)$$

from which it follows that

$$p/c \gg 1 - p \Rightarrow E[S(1)] \ll S_{tot}$$
$$p/c \ll 1 - p \Rightarrow E[S(1)] \approx S_{tot}$$

Let z denote the slope of the log-log species-area curve, evaluated at $k = 1$. By differentiating equation 9.15, we obtain

$$(9.17) \qquad z \equiv \frac{d \log E[S(1)]}{d \log k}$$
$$= -\log \left(\frac{p}{p + c - pc} \right) \frac{p}{c(1 - p)}$$

Figure 9.2B shows that this is also determined primarily by the ratio p/c. When $p/c \ll 1$, the slope approaches 0, and species number accumulates only slowly with increasing area. The "canonical" value of $z \approx 0.25$ corresponds to $p/c \approx 0.1$; i.e., to a time scale for disturbance an order of magnitude larger than that for colonization.

Local versus Regional Regulation of Diversity. Consider now the slope b of the regression of local diversity on regional diversity. This regression has been used as a test for the importance of local processes (Ricklefs 1987). If we measure local diversity by $E[S(1)]$ and regional diversity by the species pool S_{tot}, this slope is

$$(9.18) \qquad b = \frac{\partial E[S(1)]}{\partial S_{tot}}$$

Because this model contains no within-patch limitations on coexistence, it comes as no surprise that equation 9.16 shows that local diversity is directly and linearly propor-
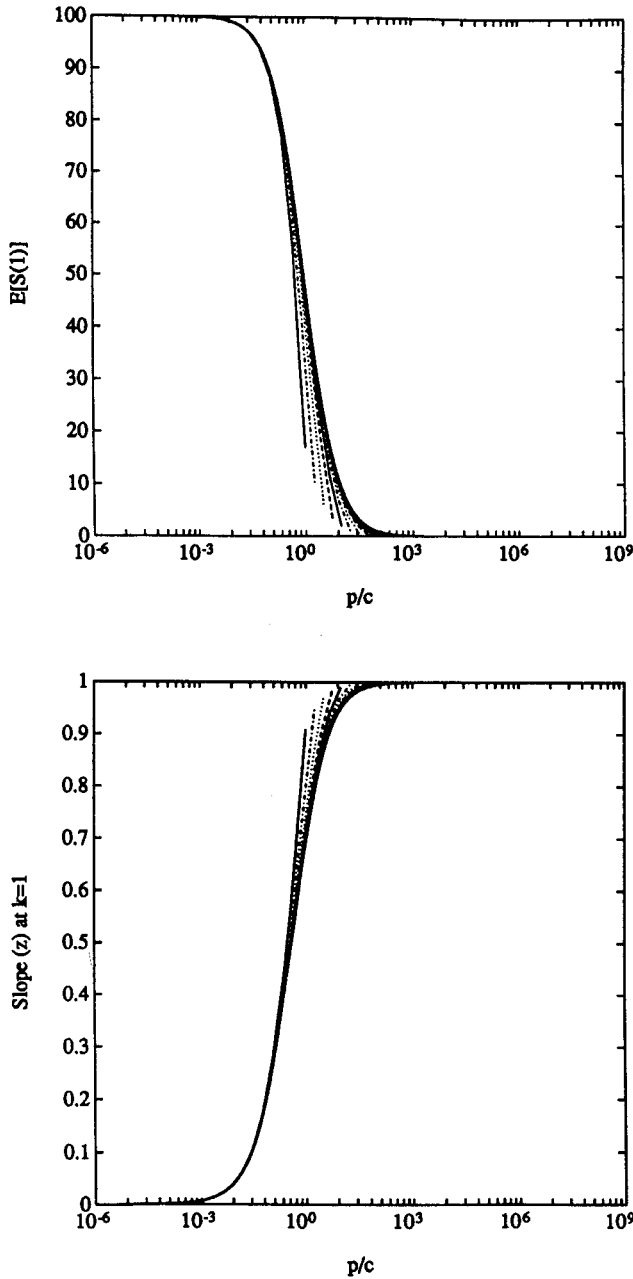
Figure 9.2 *Top:* The intercept, defined operationally as $E[S(1)]$, of the species-area curve for the noncompetitive model as a function of the ratio p/c, for $p,c \in [10^{-6},1]$. *Bottom:* The slope of the log-log species-area curve for the noncompetitive model, evaluated at $k = 1$. The slope is shown as a function of the ratio p/c, for $p,c \in [10^{-6},1]$. $S_{tot} = 100$ in both graphs.

tional to the regional species pool S_{tot}. Thus data showing that local diversity is proportional to regional diversity (Cornell 1985a, 1985b, Ricklefs 1987) are indeed compatible with an unsaturated community.

Because the slope b is given by the right-hand side of equation 9.16 when $S_{tot} = 1$, figure 9.2A can be interpreted as a plot of b, by rescaling the ordinate from zero to one. The empirical regressions interpreted in the literature

as showing lack of saturation have slopes[1] ranging from $b = 0.14$ to $b = 0.49$. In our model, these slopes correspond to $p/c \approx 0.5$.

COMPETITIVELY SATURATED COMMUNITIES

We turn now to a model with strong local competitive saturation, with the hope of distinguishing it from the noncompetitive model. Suppose that local niche space becomes saturated as one species (call it species 1) excludes all other species. In addition to the terms defined in the previous section, we define v as the rate of competitive exclusion, by species 1, of all other species present in a patch. We begin with the basic relationship

$$(9.19) \quad E[S(k)] = \sum_{t_1=0}^{\infty} \cdots \sum_{t_k=0}^{\infty} E[S(k)|D(t_1, \ldots, t_k)] \\ \times P[D(t_1, \ldots, t_k)]$$

The conditional expectation $E[S(k)|D]$, where D abbreviates $D(t_1, \ldots, t_k)$, is

$$(9.20) \quad E[S(k)|D] = \sum_{i=1}^{S_{tot}} P[\text{sp. } i \text{ present in} \geq 1 \text{ patch}|D]$$

$$(9.21) \quad = \sum_{i=1}^{S_{tot}} (1 - P[\text{sp. } i \text{ absent from all} \\ k \text{ patches}|D])$$

The conditional probability that species 1 is absent from all k patches is

$$(9.22) \quad P[\text{sp. 1 absent}|D] = (1 - c_1)^T$$

where $T = \sum_i t_i$ as before. For the other species,

$$(9.23) \quad P[\text{sp. } i, i \geq 2, \text{ absent}|D] = \\ \prod_{j=1}^{k} P[\text{sp. } i \text{ absent from patch } j|D]$$

The probabilities $P[\text{sp. } i \text{ absent from patch } j|D]$ for $i \geq 2$ depend on whether species i has colonized, whether species 1 has also colonized, and if so, whether competitive exclusion has occurred.

Consider patch j, $j = 1, \ldots, k$. Three mutually exclusive and collectively exhaustive events may be identified: (1) species 1 has not colonized, (2) species 1 colonized at some time $-\tau$ and competitive exclusion has occurred, and (3) species 1 colonized at some time $-\tau$, but competitive exclusion has not yet occurred. The probabilities of these three events are, respectively,

$$P[\text{event 1}] = (1 - c_1)^{t_j}$$

$$(9.24) \quad P[\text{event 2}] = \sum_{\tau=0}^{t_j-1} c_1(1 - c_1)^{t_j - \tau - 1}[1 - (1 - v)^{\tau}]$$

$$P[\text{event 3}] = \sum_{\tau=0}^{t_j-1} c_1(1 - c_1)^{t_j - \tau - 1}(1 - v)^{\tau}$$

The conditional probabilities of absence of species i, $i \geq 2$, are

---

1. Cynipid gall wasps (rare), $b = 0.14$; cynipid gall wasps (common), $b = 0.35$; cynipid gall wasps (total), $b = 0.49$ (Cornell 1985b); Caribbean island birds, $b \approx 0.22$ (Ricklefs 1987)

$$P[\text{sp. } i \text{ absent}|\text{event 1, } D] = (1 - c_i)^{t_j}$$
(9.25) $$P[\text{sp. } i \text{ absent}|\text{event 2, } D] = 1$$
$$P[\text{sp. } i \text{ absent}|\text{event 3, } D] = (1 - c_i)^{t_j}$$

To make the notation easier, define

(9.26) $A(i,j) = P[\text{sp. } i \text{ absent from patch } j | D]$

Then we combine equations 9.24 and 9.25 to obtain, for $i \geq 2$,

$$(9.27)\ A(i,j) = (1 - c_1)^{t_j}(1 - c_i)^{t_j} + \sum_{\tau=0}^{t_j-1} c_1(1 - c_1)^{t_j-\tau-1}$$
$$\times [(1 - v)^\tau(1 - c_i)^{t_j} + 1 - (1 - v)^\tau]$$

which, after some tedious algebra, simplifies to

$$(9.28)\, A(i,j) = 1 + [(1 - c_i)^{t_j} - 1]$$
$$\times \left[\frac{c_1(1 - v)^{t_j} - v(1 - c_1)^{t_j}}{c_1 - v} \right] \quad i \geq 2$$

In the case where $c_1 = v$, the result is

$$A(i,j) = 1 + (1 - c_1)^{t_j}$$
$$(9.29)\qquad \times \left\{ (1 - c_i)^{t_j} + \frac{t_j c_1}{1 - c_1}[(1 - c_i)^{t_j} - 1] - 1 \right\}$$
$$i \geq 2$$

The probability of absence for species 1 is given by equation 9.22:

$$(9.30)\qquad\qquad A(1,j) = (1 - c_1)^T$$

We finally get our species-area relationship

$$(9.31)\ E[S(k)] = \sum_{t_1=0}^{\infty} \cdots \sum_{t_k=0}^{\infty} [S_{\text{tot}} - \sum_{i=1}^{S_{\text{tot}}} \prod_{j=1}^{k} A(i,j)]$$
$$\times P[D(t_1, \ldots, t_k)],$$

where $P[D(t_1, \ldots, t_k)] = p^k(1 - p)^T$.

Results for Competitively Saturated Communities

Equation 9.31 reveals little about the form or behavior of the species-area relationship. To study it numerically, we used a Monte Carlo approach. For each value of k, disturbance histories were sampled by drawing k independent random variables from a geometric distribution with parameter p. The conditional expectation of $S(k)$, given this disturbance history, was calculated and the unconditional expectation obtained by averaging over a large number of disturbance histories.

Species-Area Relationships. The species-area relationship in this model is similar to that in the noncompetitive model (fig. 9.3). The curves are nearly linear on a log-log plot for small sample sizes, and asymptotic at S_{tot} as sample size increases. The parameters c, v, and p interact to determine the location of the curve. As might be expected, increasing v reduces diversity, regardless of the values of the other parameters. When disturbance is low ($p = 0.01$) increases in c increase diversity when $v = 0.011$ and decrease diversity when $v = 0.11$. This reflects the fact that c is the rate of colonization for the superior competitor as well as for all other species. When competitive exclusion is slow, the increase in colonization by competitively inferior species makes up for the increase in colonization by the competitive dominant. But when exclusion is fast, the primary effect of increased c is more rapid colonization by the superior competitor, with a consequent reduction in diversity. At a higher disturbance probability ($p = 0.1$), diversity increases with increasing c, regardless of the value of v.

Disturbance has a marked effect on diversity for any value of k (fig. 9.4). Diversity is maximized at an intermediate frequency of disturbance, and increases with the colonization rate c and decreases with the competitive exclusion rate v. As v increases, the frequency of disturbance
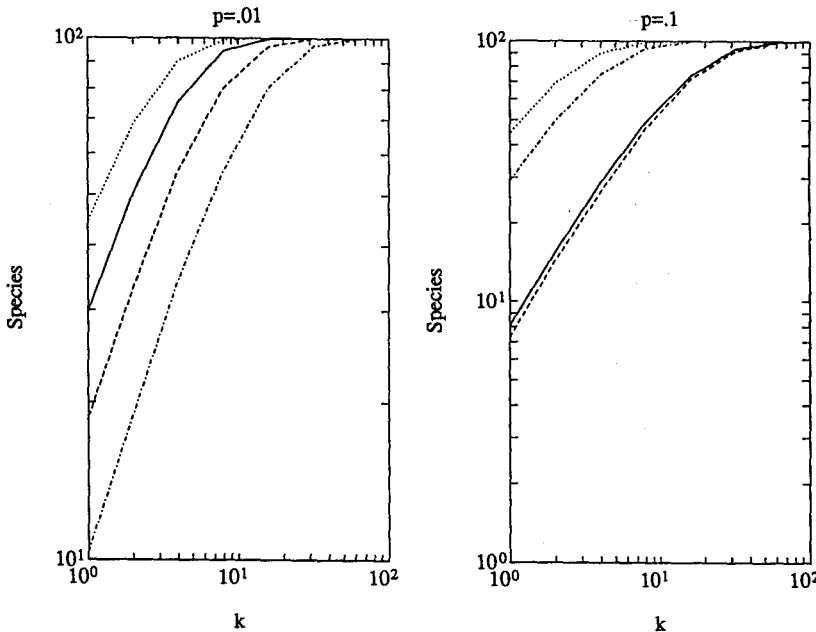

Figure 9.3 Species-area curves for the model with local competitive saturation. Parameter values (c,v) are: solid line = (.01, .011); dashed line = (.01, .11); dotted line = (.1, .011); dash-dot line = (.1, .11). $S_{\text{tot}} = 100$ throughout.
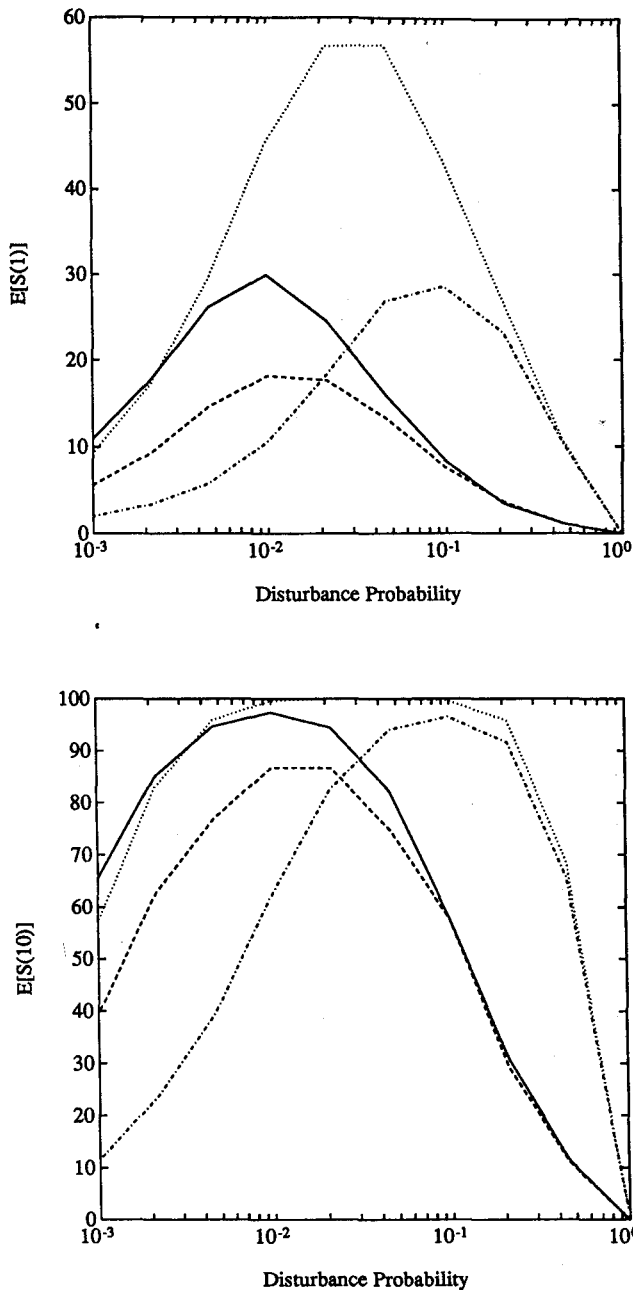
Figure 9.4 Effects of disturbance probability on species richness ($E[S(k)]$) for $k = 1$ (*upper*) and $k = 10$ (*lower*). Parameter values (p,c) are: solid line = (.01, .011); dashed line = (.01, .11); dotted line = (.1, .011); dash-dot line = (.1, .11). $S_{tot} = 100$ throughout.

needed to maximize diversity increases. These results are similar to those of the dynamic patch-occupancy models in Caswell and Cohen (1991a, 1991b).

Local versus Regional Regulation of Diversity. In the absence of disturbance, competitive saturation in this model limits local diversity to $E[S(1)] = 1$, independent of S_{tot}. Thus the slope b of the regression of local diversity on the regional species pool should equal zero. Disturbance perturbs this situation, perhaps sufficiently to obscure the

action of competition. We can investigate this by examining how b varies with p, c, and v.

Equation 9.31 can be simplified to give an analytical expression for $E[S(1)]$. Let $\bar{p} = 1 - p$, $\bar{c} = 1 - c$, and $\bar{v} = 1 - v$. Then some tedious algebra yields

$$(9.32) \quad E[S(1)] = 1 - \frac{p}{1 - \bar{p}\bar{c}} + \frac{p(S_{tot} - 1)}{c - v}$$
$$\times \left(\frac{c}{1 - \bar{p}\bar{v}} - \frac{c}{1 - \bar{p}\bar{c}\bar{v}} - \frac{v}{1 - \bar{p}\bar{c}} + \frac{v}{1 - \bar{p}\bar{c}^2} \right)$$

Figure 9.5 plots local diversity ($E[S(1)]$) as a function of both disturbance probability p and the regional species pool S_{tot}. Four combinations of the colonization probability c and the exclusion probability v are shown; in every case local diversity depends on the regional species pool (i.e., $b > 0$) except at the lowest disturbance rates. At some intermediate disturbance rate, there is a relation between local and regional diversity every bit as strong (i.e., with a value of b as large) as that produced by the noncompetitive model (equation 9.16).

The slope b of the relation between $E[S(1)]$ and S_{tot} can be obtained directly from equation 9.32; this slope is shown as a function of disturbance probability in figure 9.6. At sufficiently small values of p, $b \to 0$ as local diversity is limited by competition. As p approaches 1, $b \to 0$ as all species are eliminated by disturbance. At some intermediate frequency of disturbance, b is maximized.

When b is maximized, the community appears as unsaturated as it can be, given its values of c and v. How much disturbance is required to produce this result? The disturbance frequency p_{max} that maximizes b depends on c and v. To study this dependence we define a new rate, ρ, for the combined processes of colonization *and* competitive exclusion. A patch reaches equilibrium after species 1 has colonized and excluded all other species. The expected time required for these two processes is $1/c + 1/v$. The rate for the combined process is the inverse of this time scale:

$$(9.33) \quad \rho = \left(\frac{1}{c} + \frac{1}{v} \right)^{-1}$$

We used a Monte Carlo procedure to evaluate the relationship between p_{max} and ρ. We generated 500 random combinations of c and v, each log-uniformly distributed over the interval $[10^{-6},1]$, and calculated the resulting p_{max}.

To a good approximation, $p_{max} \approx 2\rho$ (i.e., the median value of p_{max}/ρ was 1.867, and in 78% of the cases, $1.2 < p_{max}/\rho < 10$). Thus the community appears most *un*saturated when the rate of disturbance is of the same order of magnitude as the rate of transition from an empty patch to competitive equilibrium. This is quite a low disturbance rate (measured, as it must be, relative to the other time scales in the system). For example, if $p_{max} = 2\rho$, in fully one-third of all cases, colonization and exclusion will proceed to equilibrium before the first disturbance occurs.

The slopes at the critical disturbance probability p_{max} in figure 9.6 all fall within the range of values accepted as evidence for nonsaturation by Cornell (1985b) and

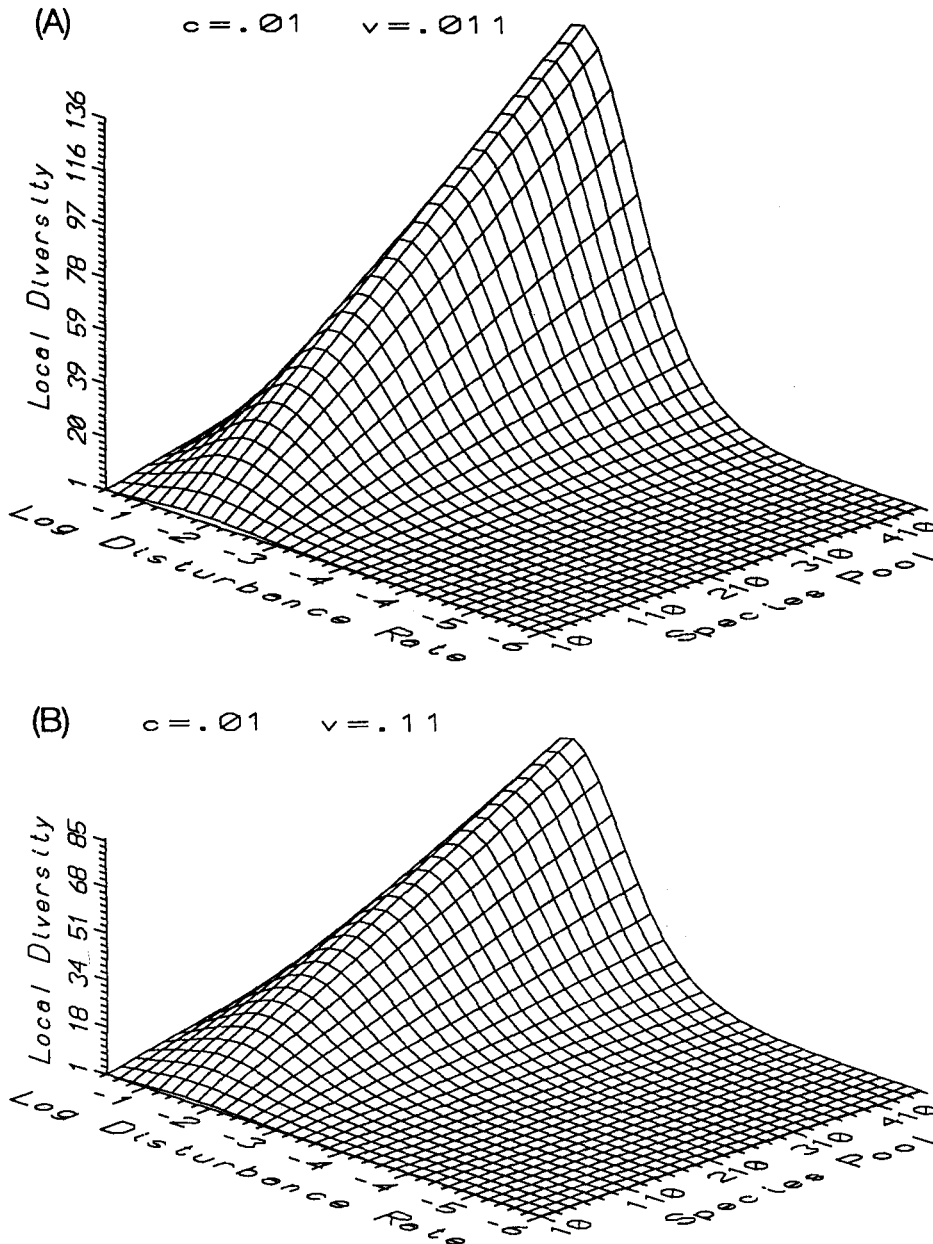(A) c = .01 v = .011

(B) c = .01 v = .11

Figure 9.5 Plots of local species diversity ($E[S(1)]$) as a function of the disturbance probability p and the regional species pool S_{tot} for four combinations of the colonization rate c and the competitive exclusion rate v. (A) $(c,v) = (.01, .011)$; (B) $(c,v) = (.01, .11)$; (C) $(c,v) = (.1, .011)$; (D) $(c,v) = (.1, .11)$; log $= \log_{10}$.

Ricklefs (1987). In fact, the slope at p_{max} in our 500 Monte Carlo samples is bounded below by 0.17, implying that, at p_{max}, practically any combination of c and v will produce a slope indicative of a noncompetitive community.

An alternative is to ask how large p must be, relative to ρ, to yield a slope large enough that it would be accepted as evidence of regional rather than local control (say, $b = 0.1$). In our Monte Carlo calculations, the ratio p/ρ producing a slope of $b = 0.1$ ranged from 0.1 to 0.4. The corresponding probabilities of reaching equilibrium before the first disturbance are 0.91 and 0.71.

In summary, even though this model includes a strong form of competitive saturation, even low rates of disturbance can completely obscure the role played by competitive saturation.

Our conclusions here are based on expected species richness. Patterns in the variance of species richness, or in the similarity among patches, may help to distinguish the effects of competition and disturbance. We have made some progress in this direction and will report the results elsewhere.
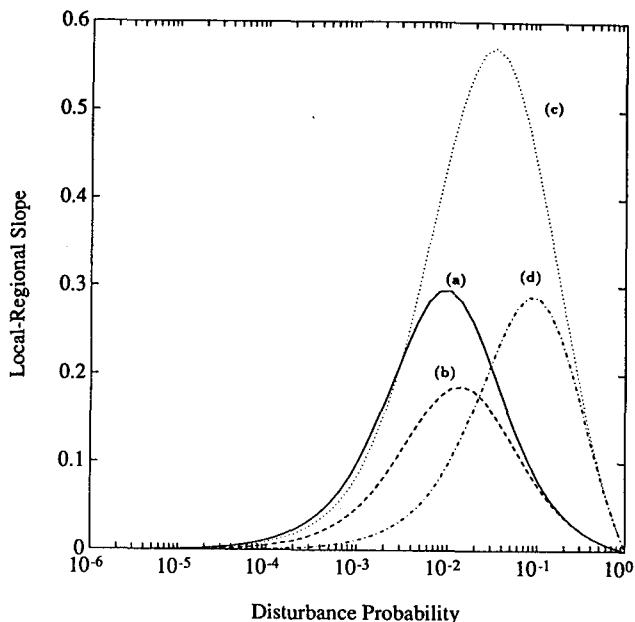
(C)

$c = .1$ $v = .011$

(D)

$c = .1$ $v = .11$
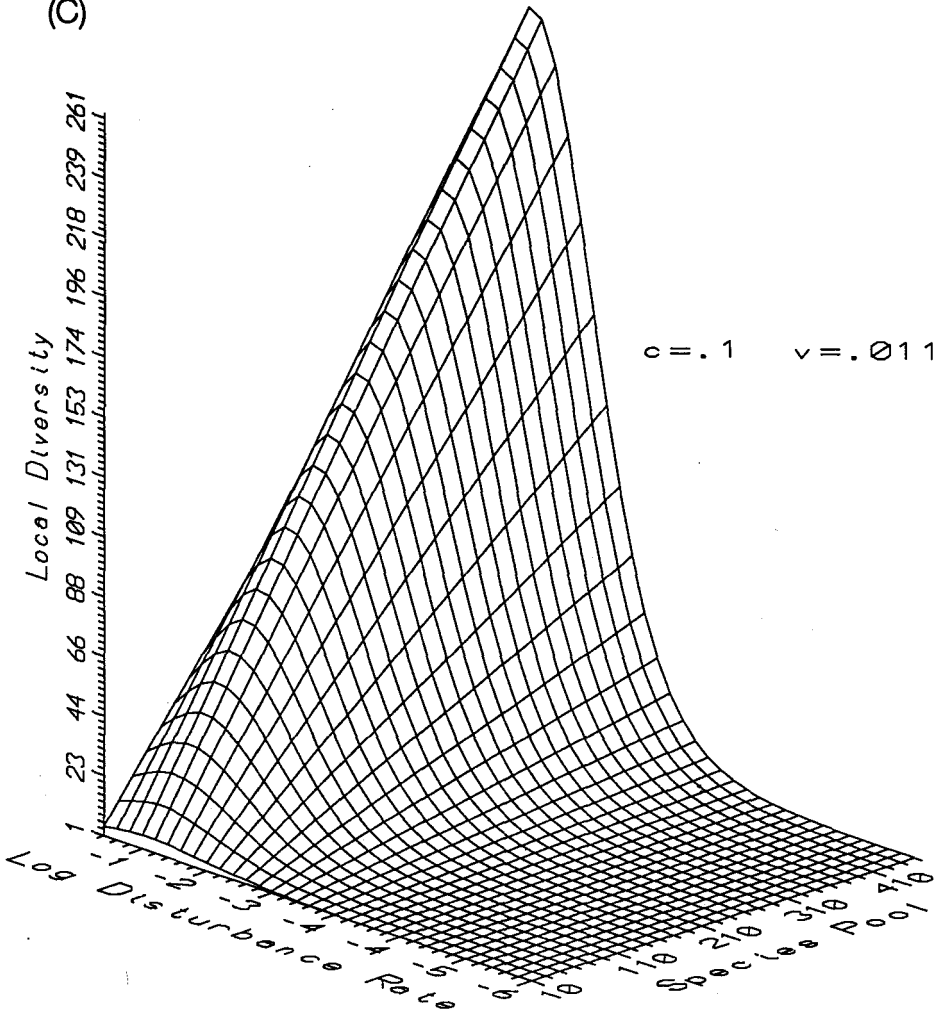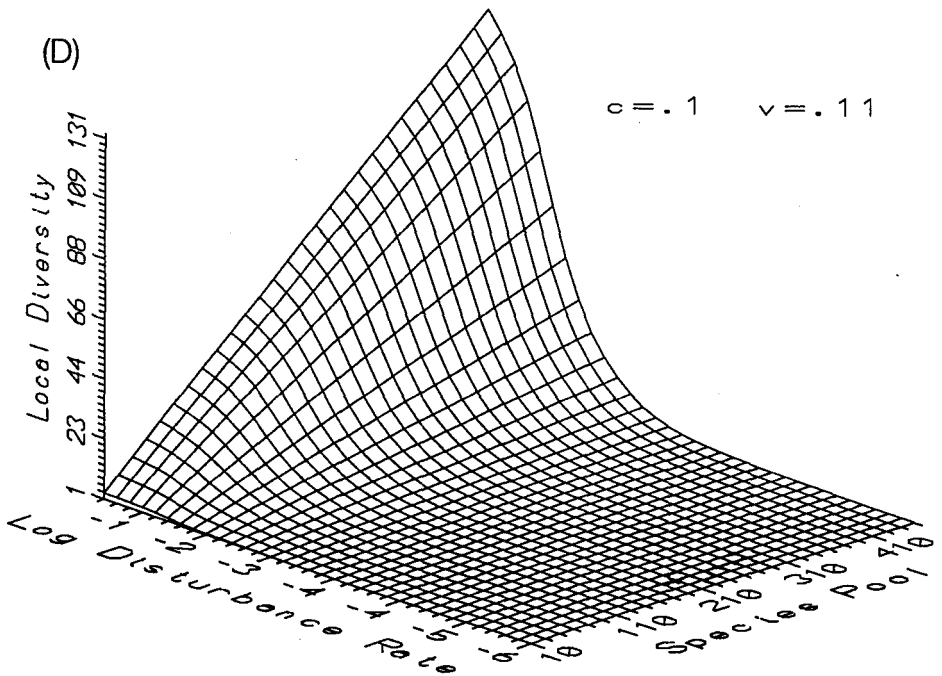
Figure 9.6   The slope of the line relating local diversity ($E[S(1)]$) to the regional species pool S_{tot}, as a function of the disturbance probability p. For (a), $(c,v) = (.01, .011)$; (b), $(c,v) = (.01, .11)$; (c), $(c,v) = (.1, .011)$; (d), $(c,v) = (.1, .11)$.

CONCLUSIONS

1. A simple path-occupancy model produces quite realistic-looking log-log species-area curves at small sample sizes, eventually becoming asymptotic to the regional species pool as the sample becomes large enough to include all the species.

2. In communities without competition, the slope of the species-area curve is an increasing function of the ratio of the disturbance rate to the colonization rate. The intercept, which measures diversity in a single patch, is a decreasing function of this same ratio.

3. In the absence of competition, local diversity is directly proportional to that of the regional species pool.

4. When competitive saturation is added to the model, the relation between local and regional diversity depends on the disturbance rate. Local diversity is independent of the regional species pool, provided that the disturbance rate is sufficiently low, but the effects of even strong competitive saturation can be obscured by extremely low rates of disturbance. Rates of disturbance one-half to one-tenth of the rate of approach to local equilibrium produce communities where local diversity is directly proportional to that of the regional species pool, with slopes comparable to those found in empirical studies interpreted as evidence of unsaturation.

5. Empirical studies relating local and regional diversity must be interpreted with caution, because the absence of competition has effects that are indistinguishable from those of strong competitive saturation in the presence of modest levels of disturbance. Future empirical studies of local and regional diversity should include quantitative measurements of the rates of disturbance, competition, and other dynamic processes.

Species Diversity in Ecological Communities

HISTORICAL AND GEOGRAPHICAL PERSPECTIVES

EDITED BY

Robert E. Ricklefs
and
Dolph Schluter