SCALE DEPENDENCE AND THE SPECIES-AREA RELATIONSHIP

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Abstract.—The complex relationship between species richness and area can be simplified by decomposing spatial scale into its components: grain, extent, and number of samples. We designed a 256 × 256-m study grid in the Oosting Natural Area in the Duke Forest, Orange County, North Carolina, such that the effects of these components can be disentangled. We found that grain, extent, and the number of samples all influenced the species-area relationship, although the effects of grain were dominant. We also found that species richness patterns were neither self-similar nor hierarchical. The degree to which diversity occurs in "hot spots" increases as a function of both grain and extent, but diversity hot spots tend to persist across a wide range of grains.

Understanding how and why species richness varies over space and time is a major endeavor in ecology. One of the most studied relationships in all of ecology is that between species richness and area sampled, or the species-area curve. The shape of the species-area curve has been used to infer biological processes such as disturbance (Lawrey 1991), competition (Lepš 1990), and division of niche space (Sugihara 1980). The relationship has been used to define the "minimum area" of a community and thus as a tool for delineating community types (Cain 1938; Rice and Kelting 1955; Oosting 1956; Goldsmith and Harrison 1976; Kershaw and Looney 1985; Colinvaux 1993). The species-area curve is central to the theory of island biogeography (MacArthur and Wilson 1963, 1967; MacArthur 1965; Patrick 1967; Williamson 1981, 1988) and hence also to the science of preserve design (Diamond and May 1981; Higgs 1981; Dzwonko and Loster 1989; Bierregaard et al. 1992). Furthermore, the species-area curve has been proposed as a means to estimate the biodiversity of large regions or preserves (Evans et al. 1955; Williams 1964; Kilburn 1966; Hubbell and Foster 1983; Lauga and Joachim 1987; Westfall et al. 1987; Gentil and Dauvin 1988; May 1988; Palmer 1990*a;* Gitay et al. 1991; Grassle and Maciolek 1992).

Numerous attempts have been made to find the functional form of the species-area curve (see, e.g., Gleason 1922, 1925; Arrhenius 1923; Williams 1964; Williamson 1981); some of these functions are justified theoretically (Williams 1964; May 1975; Coleman 1981; Williamson 1981). Despite the theoretical, historical, and applied importance of the species-area curve, it is very difficult to predict a

priori what the functional form of the relationship should be (Williams 1964; Williamson 1981). To a large degree, this is because area itself is a complex variable. While some authors believe that area (or, more generally, spatial scale) should be determined according to the properties of organisms (Addicot et al. 1987; Morris 1987; Cornell and Lawton 1992; Fahrig 1992), others argue that scale should be studied operationally (i.e., investigator defined) so that pattern can be inferred later (Allen 1987; Turner et al. 1989*a*, 1989*b*; Reed et al. 1993); we employ the latter approach here.

Spatial scale can be decomposed into several components (Addicot et al. 1987; Turner et al. 1989*b*; Kotliar and Wiens 1990; Allen and Hoekstra 1991; Milne 1991; Reed et al. 1993). The minimum scale sampled (often the size of individual quadrats) in a study is considered the grain. The maximum scale (e.g., the farthest distance between quadrats) is the extent. The number of sampled units is another important component. Other components of scale (not considered in this article) include the shape of quadrats and geometry of placement. Scale dependence is defined as the degree to which ecological phenomena vary as a function of grain, extent, or other components of scale.

The purpose of this article is to evaluate the scale dependence of species richness in a forest that is sampled at a series of different grains and extents. We intend to demonstrate that species-area curves can have a wide range of shapes within a single tract of forest and that although it is useful to decompose scale into its components, it is the interaction between the components that determines the overall relationships. In particular, we address the following questions: To what degree is the species-area relationship influenced by grain versus extent versus the number of quadrats? Does species richness vary more or less than random expectation, and does this variation depend on grain and/or extent? Do spots of particularly high (or low) richness tend to persist across spatial scales? Is spatial variation in richness self-similar, hierarchical, or neither?

STUDY SITE

This study was performed in the Oosting Natural Area, part of the Duke Forest in Orange County, North Carolina. The Natural Area consists of a heterogeneous assemblage of forest communities, some dominated by species typical of anthropogenic disturbance (e.g., *Pinus taeda, Liriodendron tulipifera*), some dominated by mesic forest species (e.g., *Acer rubrum, Liquidambar styraciflua, Fagus grandifolia*), and some tending more toward the xeric (*Quercus alba, Quercus rubra, Carya tomentosa*). However, community boundaries in the Oosting Natural Area range from poorly delineated to nonexistent. The study site is described in more detail by Reed et al. (1993).

FIELD METHODS

Although quadrats or relevés are often subjectively placed within homogeneous regions (Braun-Blanquet 1932; Kilburn 1966; Mueller-Dombois and Ellenberg 1974; Kershaw and Looney 1985; Allen and Peet 1990), such placement is not
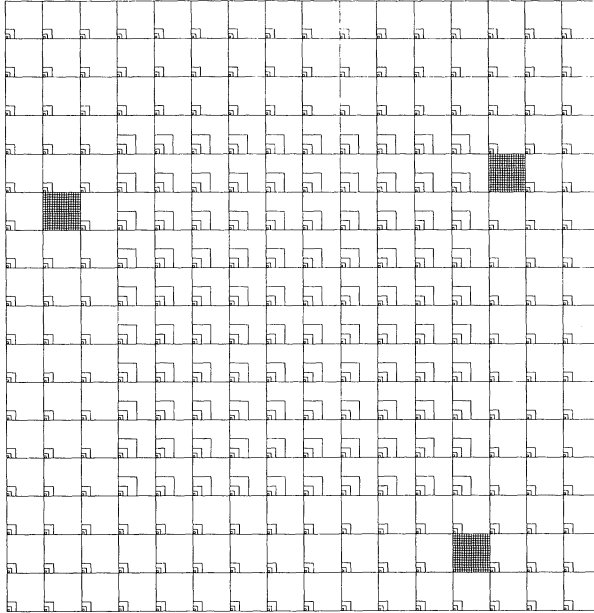
FIG. 1.—Diagram of the study grid

always desirable. In particular, since heterogeneity of sites may be a major deter-minant of the species-area relationship (Williamson 1981, 1988; Brown 1988), it is essential that the location of the study site not be based on the assumption of homogeneity. This is especially important since few landscapes consist of homogeneous habitats. The sampling grid was randomly located, with the only constraint being that it fit entirely within the preserve. Most of the major habitats in the preserve (except for young pine forests and broad floodplains) are repre-sented in the study grid.

The sampling grid consists of 256 16 × 16-m modules (fig. 1). A nested series of square quadrats (with linear dimensions of 0.125 m, 0.25 m, 0.5 m, 1 m, 2 m, and 4 m) is located in the southwestern corner of each module. Larger quadrats (with dimensions of 8 m and 16 m) were studied in the central 100 modules of the grid. Three modules (the three fine grids in fig. 1) were randomly selected for more intensive study: in these, every square meter (including quadrats of dimen-sions 0.125 m, 0.25 m, and 0.5 m nested in the southwest corner) was studied. There are thus three distinct data sets: all 256 modules, the central 100 modules, and the three fine-scale grids. If the results from the different data sets are qualita-tively similar, we will only report on one of them.

In the remainder of this article, the size of each nested quadrat will be consid-ered the quadrat's level; see table 1 for details. In May and June of 1989, the presence of each vascular plant species was recorded for each of the quadrats described above. This time was chosen because the remains of spring ephemeral plants and the first leaves of late-season plants are both clearly identifiable (those

TABLE 1

THE LEVEL AND SIZE OF QUADRATS USED IN THE
GRID ILLUSTRATED IN FIGURE 1

Level	Linear Dimensions (m)			Area (m²)
1	.125	×	.125	1/64
2	.25	×	.25	1/16
3	.5	×	.5	1/4
4	1.0	×	1.0	1
5	2.0	×	2.0	4
6	4.0	×	4.0	16
7	8.0	×	8.0	64
8	16.0	×	16.0	256

late-season plants that were difficult to identify, particularly graminoids and com-
posites, were flagged in May and June and identified later during several return
trips in autumn).

Grain and extent are areal concepts, but they are more conveniently expressed
in terms of linear measurements for the purposes of this study. By choosing the
size of quadrats in the study and/or by selectively aggregating adjacent modules,
grain can vary from 0.125 m to 160 m (equivalent to the completely inventoried
central area of 10×10 modules). Extent can vary from 2 m (by studying adjacent
1×1-m quadrats in any of the three intensive modules) to 256 m. Note: in this
study, "extent" is considered the maximum distance between quadrats in the
N-S and E-W directions; technically the extent could reach 256^2 m in the NE-SW
or NW-SE direction.

Spatial Dependence and Statistics

Although the research design allows for a range of grains and extents, statistical
inference is limited because quadrats are not independent (this is a limitation of
any spatially based study, not just this one). Spatially based sampling typically
reveals spatial dependence (Burrough 1983a, 1983b, 1987; Palmer 1988, 1990b;
Legendre and Fortin 1989; Palmer and Dixon 1990; Lechowicz and Bell 1991),
which means that nearby quadrats are on the average more similar to each other
than distant quadrats. Any study with nested quadrats runs into another kind of
dependence: the data present in one grain contribute to the data of the next
highest grain. Unless somehow corrected, any kind of dependence in data will
make inferential statistics (i.e., the use of P values) biased. The analyses used
here in comparing grain and extent are of necessity complex, and it is unclear how
one would correct for dependent data. Therefore, the results will be presented for
their descriptive value only, and no formal attempt will be made to test statistical
hypotheses.

RESULTS

A total of 224 vascular plant species were encountered in the study grid, repre-
senting approximately 23% of the species present in the Duke Forest (Palmer

TABLE 2

THE MOST FREQUENT SPECIES ENCOUNTERED IN QUADRATS OF LEVEL
6 OF ALL 256 MODULES

Taxon	No. of Quadrats
Acer rubrum L.	256
Cornus florida L.	249
Desmodium nudiflorum (L.) DC	242
Smilacina racemosa (L.) Desf.	233
Cercis canadensis L.	232
Viburnum rafinesquianum Schultes	232
Galium circaezans Michaux	228
Polygonatum biflorum (Walter) Ell.	227
Carya ovata (Miller) K. Koch	227
Vitis rotundifolia Michaux	223
Liriodendron tulipifera L.	205
Phryma leptostachya L.	200
Prunus serotina Ehrhart	200
Euonymus americanus L.	199
Botrychium virginianum (L.) Swartz	183
Liquidambar styraciflua L.	173
Parthenocissus quinquefolia (L.) Planchon	168
Quercus alba L.	147
Quercus velutina Lam.	142
Sassifras albidum (Nuttall) Nees	130
Pinus taeda L.	129
Quercus rubra L.	119
Carya tomentosa (Poiret) Nuttall	115
Juniperus virginiana L.	110
Vitis aestivalis Michaux	96
Chimaphila maculata (L.) Pursh	94
Viola pedata L.	90
Carpinus caroliniana Walter	86
Sanicula gregaria Bicknell	86
Fagus grandifolia Ehrhart	86
Morus rubra L.	85
Ruellia caroliniensis (Walter) Studel	83
Amphicarpa bracteata (L.) Fernald	82
Prenanthes altissima L.	80
Viburnum acerifolium L.	78
Carya glabra (Miller) Sweet	75
Sanicula smallii Bicknell	72
Carex nigromarginata Schweinitz	68

NOTE.—Not shown are 186 species of lesser frequency. For the most part, these species are also the most frequent at other levels and in the central 100 modules.

1990*d*). The most frequently encountered species are listed in table 2. An electronic copy of the data set is available upon request to M.W.P.

The Species-Area Curve

Even for the analysis of a single data set, there are numerous ways to construct species-area curves (Cain 1938; Williams 1964; Westfall et al. 1987; Magurran 1988; Quinn and Harrison 1988; Lawrey 1992). One method is to add quadrats

sequentially and count the cumulative number of species encountered (see, e.g., Rice and Kelting 1955; Kikuchi 1987; Magurran 1988; Thiollay 1990). Since this method is highly sensitive to the order in which quadrats are added, we chose to calculate the average of the species-area curves for 200 random orders of quadrats, sampled without replacement (see Palmer 1991). This was performed separately for each quadrat level (fig. 2). For ease of visual interpretation, area is plotted on a logarithmic scale.

Figure 2 illustrates that grain (level) has a profound effect on the species-area relationship. At a fixed area, decreasing grain increases the number of quadrats while at the same time increasing the number of species sampled. The curves are remarkably parallel and evenly spaced from each other. The curves for higher levels are more log-linear than those at lower levels, which indicates a profound but gradual change in slope. The curves for all 256 modules (fig. 2A) are much steeper and higher than the corresponding curves for the central 100 modules (fig. 2B). There is clearly no tendency for any of the species-area curves to level off to a horizontal asymptote.

Figure 2 also illustrates that sequentially adding nonnested quadrats causes a much faster rate of species gain than does increasing area in a series of nested quadrats (i.e., the line connecting the bottom of the curves).

Variability in species-area curves within a given level is illustrated in figure 3 for all 256 modules (the results for the central 100 modules are qualitatively similar and are not shown). These shapes can be considered "envelopes" within which almost all of the possible species-area curves would fall. The top curve for each level represents the average of the 25 highest species-area curves (out of 1,000 random quadrat sequences). The bottom curve is the average of the 25 lowest species-area curves. The fact that these curves meet toward the upper right is a trivial consequence of the fact that all quadrats at that level have been sampled. Figure 3 illustrates that variability in species-area curves can be very substantial; the envelopes for different levels can overlap considerably. However, the envelopes do not overlap at the extreme left and right ends.

Extent and Species Richness

The influence of extent on species richness can be evaluated directly by observing how the distance between one quadrat and a second effects the number of species that are present in the second quadrat but not the first (i.e., the number of "new" species). Figure 4 demonstrates that extent has practically no effect on new species at low grains but has a positive effect at large grains. Thus, there is a substantial interaction between grain and extent in determining richness.

The relative effects of grain and extent are also illustrated in figure 5. This figure represents the number of species encountered in all possible combinations of four equal-sized quadrats arranged in a square. The roughly triangular arrangement of these curves is a consequence of the fact that extent is constrained to be no less than twice the grain. The right end of these curves seem to have most variation: however, this is probably a manifestation of the "hole effect" (Journel and Huijbregts 1978; Hohn 1988; Isaaks and Srivastava 1989), a statistical artifact caused by pseudoreplication at large extents.

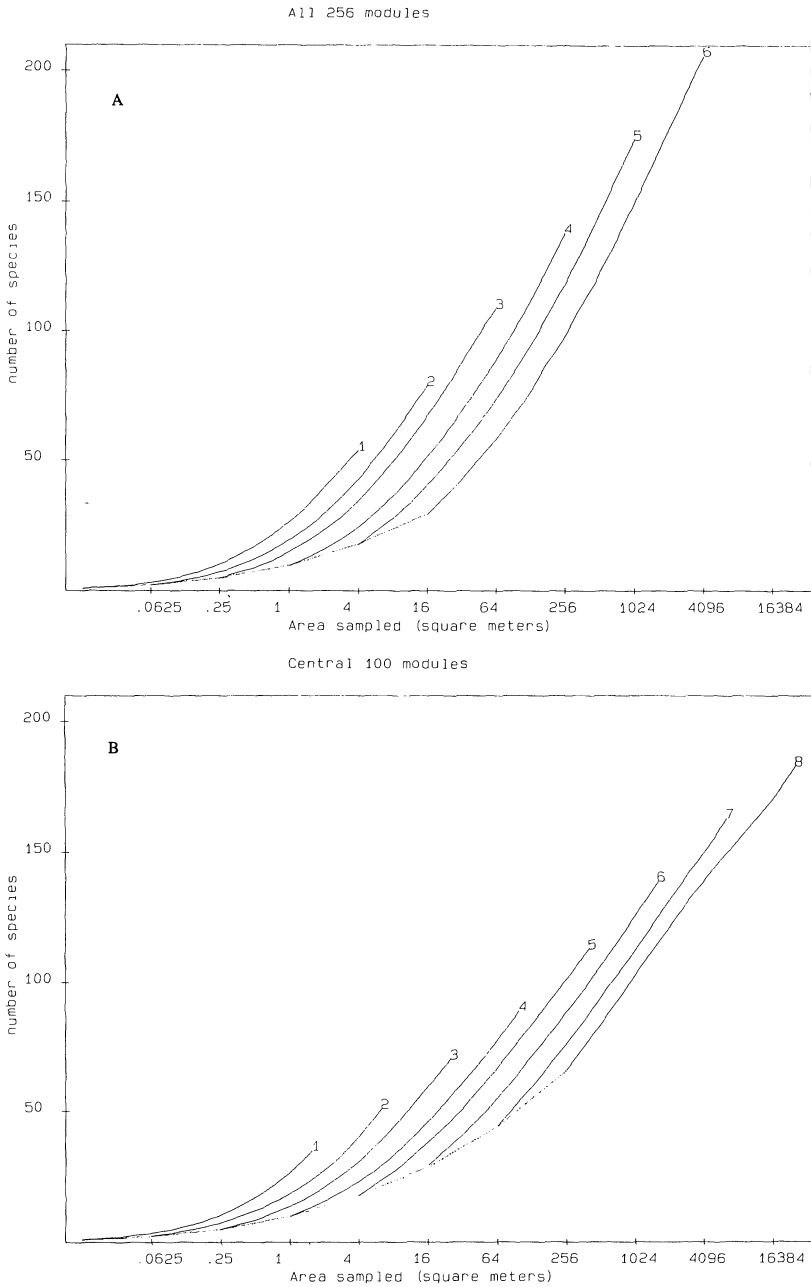All 256 modules

Central 100 modules

Fig. 2.—Species-area curves in the study grid. Each curve represents the average of 200 different species-area curves, each with a different random order of quadrats. The lighter-colored curve connecting the lower ends of each curve represents the average species-area curve obtained by expanding the level (sensu table 1) of the nested quadrats. *A*, All 256 modules; *B*, the central 100 modules. Numbers above each grid represent the quadrat level; see table 1.
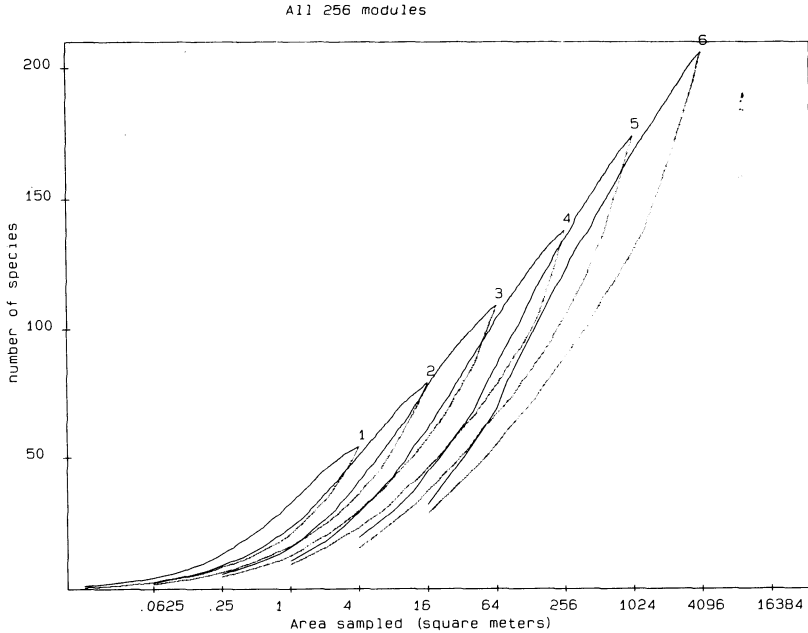
All 256 modules

FIG. 3.—Envelopes bounding species-area curves. For each level, the upper curve repre-
sents the average of the highest 25 species-area curves, and the lower curve represents the
average of the lowest 25 species-area curves, out of 1,000 separate species-area curves with
different random quadrat sequences.

In figure 5, the far left point of each curve for each level indicates the situation
in which the four quadrats are directly abutting: In other words, it is the richness
of the quadrat of the next highest level (twice the length, four times the area).
The initial slope of the curves in figure 5 is therefore not merely an effect of
extent but also an effect of disaggregation, or of making quadrats discontinuous.
    The slope gauge in the upper left of figure 5 lets us evaluate how many species
are added by doubling the linear dimensions of extent (or quadrupling the area
of extent). Extent has an effect on species richness: the curves are ascending for
most of their length. However, if we ignore the hole effect and the effects of
disaggregation, extent has only a minor effect: the slope corresponds, at most,
to around five new species per doubling. Doubling grain, on the other hand, adds
from 5–35 species, with 10–25 species being most typical.
    It is interesting that the curves for the central 100 modules and for all 256
modules largely coincide. The lack of coincidence of the larger grains in the
intensive modules with the corresponding grains for the larger grids is probably
because, by chance, the intensive modules are slightly richer than the average
module.

Variation in Species Richness

    Variation in species richness, like mean species richness, is likely to vary as a
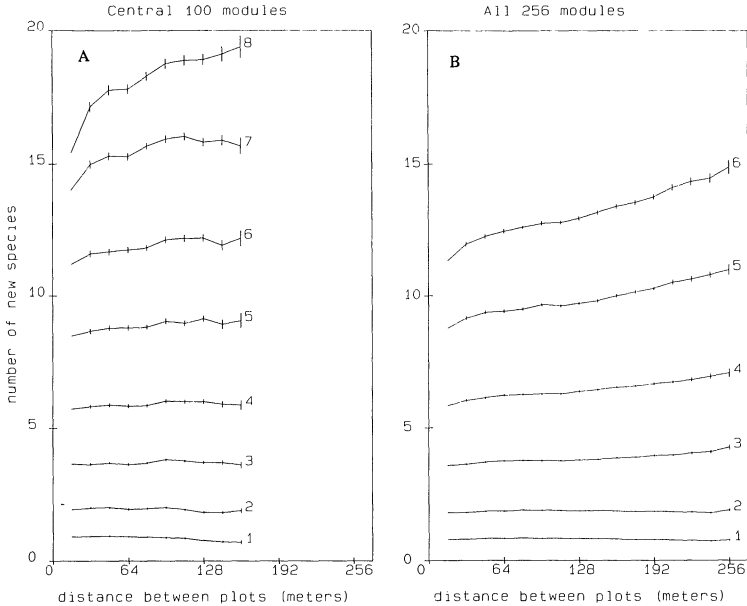function of spatial scale. The ratio of observed variance in richness to expected

FIG. 4.—The number of new species encountered in a second quadrat but not in the first, as a function of the distance between quadrats. The level is indicated by the number to the right of the curve (see table 1). These curves represent the average over all possible pairs of quadrats of a given level in a given distance class; distance classes were determined by rounding distance down to the nearest meter. Vertical bars indicate SEs of the mean. Each pair of quadrats is actually included twice, because the number of species found in A but not B is typically not the same as the number found in B but not A.

variance in richness (under the null model of no associations between species), or the variance test, is a useful way to evaluate the magnitude of variation in richness (Schluter 1984; Palmer 1987, 1990c). The expected variance in species richness under the null model (see Schluter 1984 and Palmer 1987 for justification) is calculated as $\Sigma p_i(1 - p_i)$, where p_i is the proportion of quadrats occupied by species i and the summation is over all the species in the study.

The overall study grid (fig. 1) can be decomposed into a very large number of subgrids of varying grain and extent. We can thus evaluate variation in species richness as a function of grain and extent. The results in figure 6 are for subgrids of 16 quadrats consisting of four equidistant rows and four equidistant columns, with the distance between rows equaling that between columns. Grain is the size of the quadrats, and distance is the distance between the beginning of one row (or column) and the beginning of the next row (or column). Extent is thus closely related to "distance"; namely, extent = 4 × distance + grain. The results in figure 6 represent the average of all possible subgrids of the indicated grain and distance.

Figure 6A illustrates the results of the variance test for the 16-quadrat subgrids derived from the entire 256 module study grid. In general, grains less than 1 m have values of the variance ratio close to one, which indicates that richness does
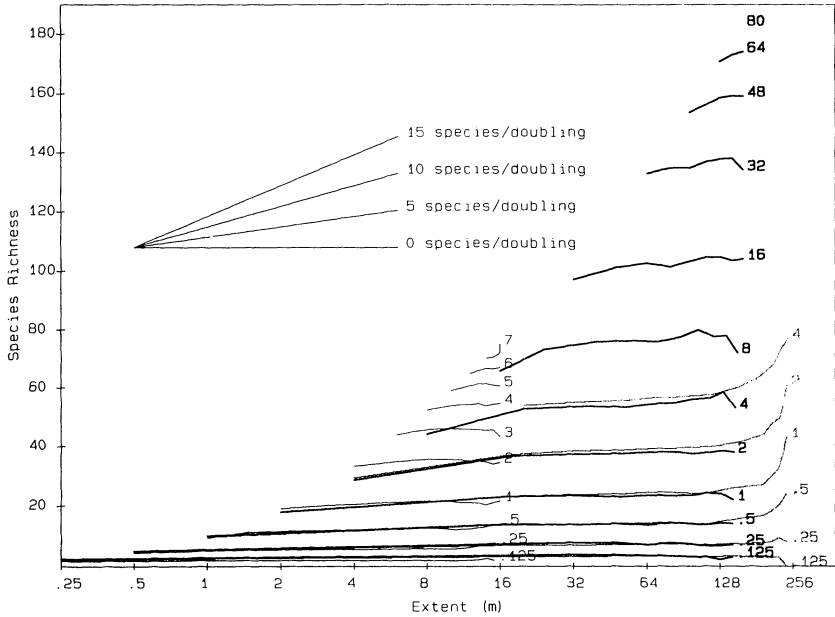
Fig. 5.—The average richness observed in all possible combinations of four equal-sized quadrats arranged in a square. Fine lines represent the average of the three intensive grids, dark thick lines represent the central 100 modules, and light thin lines represent all 256 modules. The grain, in meters, is to the right of each curve. Large grains were obtained by aggregating adjacent modules. The slope gauge in the upper left lets us evaluate how many species are added by doubling the linear dimensions of extent.

not vary much more than random expectation. However, variation in richness increases dramatically with grain, for grains of 1 m and greater. This means there is an increasing tendency for richness to occur in "hot spots" as grain increases.

As before, extent does not have as profound an effect as does grain, but when distance exceeds 48 m, species richness is much more variable than at lesser distances (at least for large grains). This means that increasing extent increases the degree to which one can find hot spots in richness.

Similar results can be seen for the central 100 modules (fig. 6B). Variation in richness is close to the null expectation for grains less than a meter, and it increases dramatically at larger grains. There is an interesting leveling off (or perhaps even a decline) in the variance ratio of grains between 4 m and 8 m and a dramatic increase at 16 m. This leveling does not imply that the size of a diversity hot spot is around 4–8 m, because the increase at 16 m suggests that hot spots are more distinctive on that scale; all it means is that diversity patterns are relatively scale-neutral at that size. As in figure 6A, there is not much difference between a distance between rows of 16 m and 32 m.

The results of the variance test for the smaller, intensive modules (not illustrated here) revealed values of the variance ratio close to one, which indicates
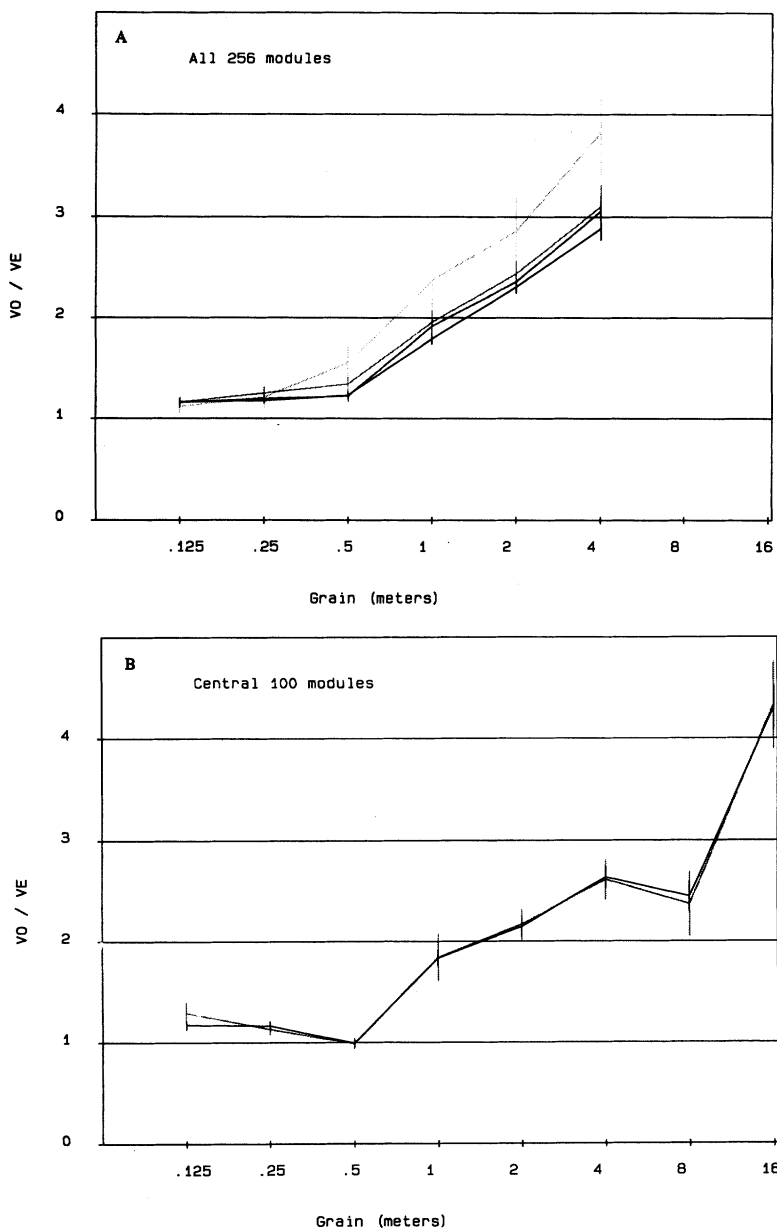
FIG. 6.—The ratio of observed species richness to expected species richness, as a function of grain. Vertical bars indicate standard errors. *A*, Results for 16-quadrat subgrids of all 256 modules. Lines ranging from dark to light indicate distances (where distance is as in fig. 6) of 16 m, 32 m, 48 m, and 64 m, respectively. *B*, Results for 16-quadrat subgrids of the central 100 modules. The dark line indicates a distance of 16 m, and the light line indicates 32 m.
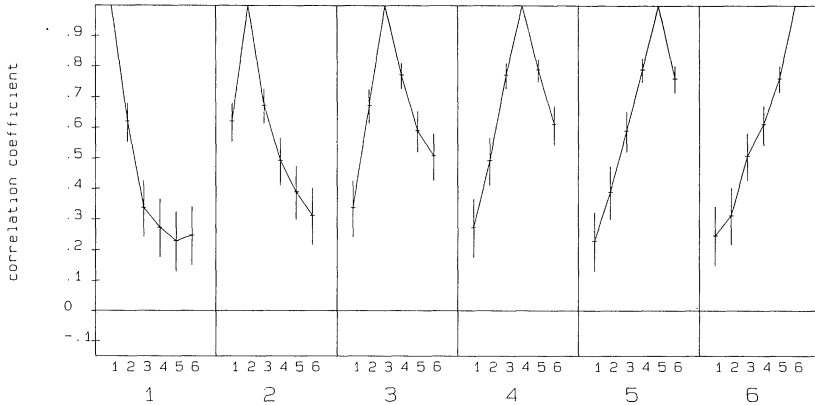
FIG. 7.—Correlation coefficients (*r*) of species richness in quadrats of one level (the single large number at the bottom of each panel) with richness in quadrats of other levels in the same module (the six smaller numbers). Vertical bars indicate 90% confidence intervals. The correlation coefficient of each level with itself is necessarily equal to one.

that richness was not more variable than random expectation. Neither grain nor extent revealed any consistent trends.

Cross-Scale Richness Correlations

Figure 7 displays the strength of correlation between species richnesses at different grains, for the data from all 256 modules. Species richness at a given grain is strongly correlated with richness at the next largest (and next smallest) grain but much less strongly correlated with richness at much larger and smaller grains. The decline in the correlation is a gradual function of change in grain. Another way of interpreting figure 7 is that diversity hot spots (regions of high richness) tend to persist (within limits) as one changes grain: a quadrat will tend to be species-rich if it is nested within a species-rich quadrat that is larger; conversely, a quadrat that includes a smaller species-rich plot will also tend to be rich. The same patterns hold for low-diversity spots. These patterns are hardly surprising and somewhat artifactual: the number of species in any quadrat is constrained to be no less than the number of species in any included quadrat.

Figure 7 also reveals that changing scale is not always symmetrical: for example, richness at level 3 is more strongly correlated with richness at level 4 than it is with richness at level 2. The decline in the correlation as one increases grain from level 1 is significantly more precipitous than the decline as one decreases grain from level 6.

Correlations for the central 100 modules (not shown) are qualitatively similar to those in figure 7. The major quantitative differences are that correlations are much weaker (probably since much less area is covered) and the confidence intervals are broader (since there are fewer samples).

Disaggregation of Quadrats

The study grid used in this research allows much flexibility in altering grain, extent, and total number of quadrats. However, these three components of area cannot be varied completely independently. For example, if the total area in a group of quadrats is held constant, decreasing grain is necessarily accompanied by an increase in number of quadrats (and increasing grain is accompanied by a decrease in number of quadrats). In this case, decreasing grain can be considered disaggregating the sampled area.

Disaggregation of area appears to have a remarkably constant effect (fig. 2). Species-area curves for different grains are parallel and evenly spaced. This means that a given amount of disaggregation is accompanied by a more or less constant increase in the number of species, over a wide range of areas sampled and grains. The constancy implies that there is some regular, underlying process relating richness to disaggregation. This process need not be complex: a number of simple processes (such as fragmentation, fracturing, curdling, and Brownian motion) have been shown to produce patterns that are constant over wide ranges of spatial scales (Burrough 1981, 1983a, 1983b; Mandelbrot 1983; Feder 1988; Petigen and Saupe 1988; Lauwerier 1991).

Zacharias and Brandes (1990) found that disaggregation had a reasonably constant effect on species richness of woodlots, on spatial scales much larger than those considered here. Dzwonko and Loster (1989) also studied woodlots on larger scales, but they found that the effects of disaggregation on richness were location- and area-dependent.

The regularity of figure 2 means we can partially decompose the species-area curve into some of its components. In particular, we can answer the following question: Given a cumulative species-area curve of randomly added quadrats with constant grain, how much of the increase is due to pure area effects, and how much is due to increasing the number of nonnested quadrats?

Figure 8 represents an idealized version of the region of figure 2 in which the species-area curves are linear, parallel, and equidistant. We wish to determine the degree to which the difference between R3 and R1 is caused by increasing area as compared to increasing number of samples. Let us define the following terms: O is the "original" number of species in N quadrats of size G; G is the grain of the square quadrat, measured in length of side; N is the number of quadrats sampled (not on the graph); A is the total area sampled, or $G^2 N$; and F is a (dimensionless) scale factor—it is the amount by which area is increased or decreased. In our study, $F = 4$ because each level is fourfold the area of the previous level. In addition, D is the number of new species encountered by disaggregating a given sample into F times the number of original quadrats (each new quadrat with an area G^2/F). Finally, S is the factor by which we would have to decrease quadrat size to have the same number of species, if the number of quadrats was increased F-fold.

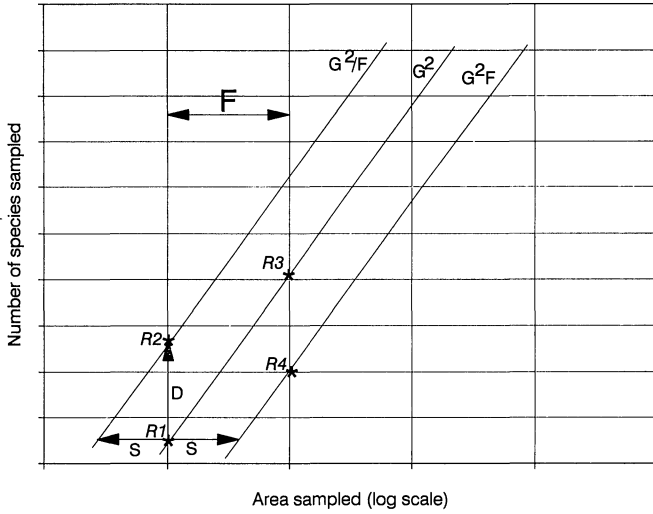Given these definitions, table 3 lists the equations for species richness of four

Fig. 8.— A schematic representation of families of species-area curves from randomly added quadrats, where quadrat area varies by a factor of F. See text for explanation of terms.

TABLE 3

Equations for Species Richness at the Four Marked Points on Figure 8

Point on Graph	Quadrat Area	No. of Quadrats	Total Area	Species Richness
R1	G^2	N	A	O
R2	G^2/F	$N \times F$	A	$O + D$
R3	G^2	$N \times F$	$A \times F$	$O + DF/S$
R4	$G^2 \times F$	N	$A \times F$	$O + DF/S - D$

Note.—The number of species is calculated on the assumption that the lines are parallel and equidistant. A is always G^2N.

points (R1–R4) illustrated in figure 8. Our original question—Given a cumulative species-area curve of randomly added quadrats with constant grain, how much of the increase is due to pure area effects, and how much is due to increasing the number of quadrats?—can now be more precisely formulated: How much of (R3 − R1) is due to increasing A by F, and how much is due to increasing N by F? The proportion due to increasing area, p_A, is

$$p_A = (R4 - R1)/(R3 - R1).$$

Substituting in the equations from table 3, this equation simplifies to

$$p_A = 1 - S/F.$$

The proportion due to increasing the number of quadrats is

$$p_N = (R2 - R1)/(R3 - R1),$$

which simplifies to

$$p_N = S/F.$$

In figure 2, p_N is the ratio of the horizontal distance between species-area curves to the horizontal distance indicating a fourfold difference in area and approximately equals 0.35. Therefore, $p_A = 0.65$.

We can conclude that most (approximately two-thirds) of the species-area curve from sequentially added quadrats is actually caused by increasing area, but the proportion caused by increasing the number of quadrats (approximately one-third) is far from negligible!

The arguments outlined above only pertain to the equidistant and parallel portions of the species-area curves, and therefore they do not explain why the overall shapes of the curves vary dramatically but gradually from small to large grains. In particular, species-area curves for small grains begin with very low slopes. To some degree, this can be considered a trivial result: since richness cannot be less than zero, a zero asymptote seems reasonable. Even so, it is theoretically possible for the curves to start near zero species and then rise with initially steep slopes.

Why does this not happen? We suspect that smaller grains are of the same magnitude as the size of individual organisms (or individual clumps of organisms) and that the total species richness is constrained by the number of individuals that can fit into the quadrat. In order to test whether this is a reasonable explanation, we performed computer simulations of species-area curves on two hypothetical landscapes: one in which each 1 m × 1 m of the landscape was randomly assigned to one of 256 species, and another in which each 4 m × 4 m of the landscape was thus assigned.

Figure 9 illustrates the species-area curves (calculated as in fig. 2) from these hypothetical landscapes. The curvilinearity of the upper portion of the some of the curves (not seen in fig. 2) may be caused by the lack of spatial trends in the simulated landscapes or by differences in the frequency distributions of species. On the other hand, the inflections in the lower part of some of the curves bear a striking resemblance to those in figure 2.

For levels much less than the size of the individual (i.e., levels 1 and 2 for both landscapes, level 3 of the large-individual landscape), the curves are almost indistinguishable. For these curves, the number of species encountered is almost solely dependent on the number of independent quadrats. As the level increases to a scale much larger than the individual, the curvilinearity of the lower part of the curve disappears (though not entirely for the large-individual landscape). The results from these simulations suggest that the average size of individual organisms or clumps (i.e., Kershaw and Looney's [1985] "morphological pattern") is a plausible explanation for the existence and position of the lower inflection in the species-area curve.
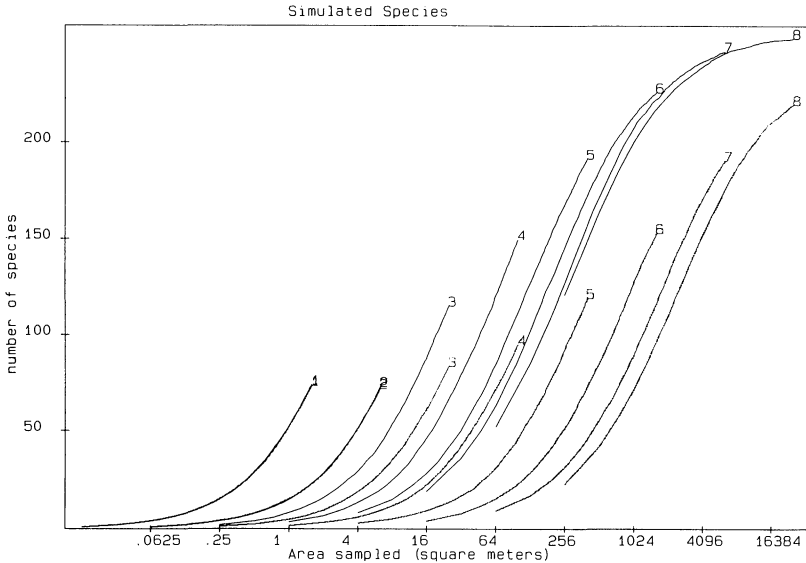
FIG. 9.—Simulated species-area curves from two hypothetical landscapes varying in the size of individuals. Curves were generated as in fig. 2. *Thin lines*, individuals are 1 m on a side; *thick lines*, individuals are 4 m on a side.

Grain and Extent

This study demonstrates that the species-area relationship is heavily influenced by grain, especially at small extents. Grain has a very strong influence on the number of species added by sampling a second quadrat (fig. 4) and on the number of species in groups of four quadrats (fig. 5). Increasing grain also strongly increases the patchiness of richness, that is, the degree to which variation in richness exceeds random variation (fig. 6).

Although grain has the largest effect, extent has an important but subtle influence. Species are added more quickly to the species-area curve if the extent is the entire study grid rather than just the central 100 modules (fig. 2). Extent increases the number of species encountered by sampling a second quadrat (fig. 4). Extent can increase the number of species encountered in subgrids of the study grid (fig. 5). Extent slightly increases the patchiness of richness (fig. 6).

The effects of extent in promoting richness are probably related to distance decay in the environment. Distance decay (also known as spatial dependence or the ''reddened spectrum'' sensu Williamson 1988) is an almost universal property of spatially based data (Burrough 1983a; Robertson 1987; Palmer 1988, 1990b, 1990c, 1992; Legendre and Fortin 1989; Lechowicz and Bell 1991) and describes the situation in which nearby environments are generally more similar to each other than distant environments. If distant environments are different, then they will on the average contain more species in aggregate than nearby environments (on the assumption that organisms exhibit some habitat or microhabitat specificity).

Grain and extent interact in affecting richness. Increasing the distance between

quadrats only increases the number of new species if the grain is large (fig. 4). The ratio of observed to expected species richness does not differ among different extents, except for large grains (fig. 6). This interaction between grain and extent demonstrates that we cannot fully understand the effects of changing scale until we understand the roles played by the different components of scale.

Scale Decay

Since the decline in the correlation between species richnesses at different grains is a gradual function of increasing or decreasing grain (fig. 7), clearly species richness is not determined by forces operating on crisply defined spatial scales. Rather, there is a "scale decay" that is directly analogous to "distance decay," and scale domains (the range of spatial scales over which a process operates) of richness are broad and poorly defined. This is consistent with results from other studies (Shmida and Wilson 1985; Auerbach and Shmida 1987; Rejmánek and Rosen 1988; Palmer 1990b, 1990c; Reed et al. 1993).

Since correlations in richness are not a symmetrical function of scale (fig. 7), we can also conclude that richness patterns are not strictly statistically self-similar in the sense of fractal geometry (Mandelbrot 1983; Feder 1988; Petigen and Saupe 1988).

Randomness on the Small Scale

The literature is ambiguous as to how spatial scale should affect the degree to which community structure departs from randomness. Some authors suggest that on the scale of individual organisms, interactions between individuals should lead to strong departures from randomness (Connor and Bowers 1987; Thórhallsdóttir 1990; Watkins and Wilson 1992). Agnew and Gitay (1990) suggest that species-rich systems should have strong small-scale structure. On the other hand, Rogers (1993) specifically looked for such small-scale patterns and failed to detect them. Ricklefs (1987) and Cornell and Lawton (1992) argue that larger-scale forces are the prime determinants of local patterns, while Willems et al. (1993) argue that an understanding of the small-scale dynamics is essential. Wiegleb et al. (1989) and Reed et al. (1993) suggest small-scale patterns may be too "noisy" to allow their detection.

The analyses presented here show that variation in species richness does not vary substantially from random expectation at small grains and extents (fig. 6). However, it is not possible to determine whether this is due to a lack of interactions among intervals or to the statistical problems of a smaller sample of individuals and species on small scales.

Spatial Hierarchies

A large body of literature suggests that the spatial structure of nature is intrinsically hierarchical (Krummel et al. 1987; Ricklefs 1987; Kotliar and Wiens 1990; Peterson and Pickett 1990; Barrangé and Campos 1991; Kolasa and Rollo 1991; O'Neill et al. 1991; Holling 1992; McLaughlin 1992). However, the analyses presented here are inconsistent with a hierarchical view of spatial pattern. There are no breakpoints or "thresholds" (sensu Gardner et al. 1989; Meentemeyer 1989) at well-defined scale intervals, within the range of spatial scales studied. The

results are more consonant with the view that patterns change gradually and continuously as a function of scale (Levin 1987; Williamson 1988; Hengeveld 1990; Lechowicz and Bell 1991; Virkkala 1991; Reed et al. 1993).

Location Dependence

As previously stated, it was extremely important for the study grid *not* to be placed using a criterion of homogeneity. As a consequence, a number of "unusual" microsites were included in the grid: a small stream runs through the southwestern corner, a ridge of basic soils (possibly an ultramafic intrusion) runs through the eastern half, and tree-fall gaps are widely scattered throughout (see Reed et al. 1993 for a more complete description).

The particular results of this study are caused by the particular spatial distributions of particular microsites. In other words, the results are location-dependent. Location dependence is particularly reflected the erratic behavior of the right end of the curves in figure 5; as previously mentioned, this behavior is termed the hole effect.

We believe that, in general, the probability of encountering unusual microsites (of any sort) in a study such as this is close to unity (by analogy, the chance of any particular coincidence occurring is vanishingly small, but since there is an astronomical number of potential coincidences, coincidences happen every day). The hole effect will never disappear, and location dependence as a phenomenon may be location-independent. To truly understand location dependence, we would need to develop an objective measure of "unusualness" and examine its geometry (which would probably have fractal attributes).

The Species-Area Curve and Conservation Biology

As the science of conservation biology is maturing, scientists are becoming increasingly aware of how little we actually know about biodiversity (May 1988; Erwin 1991; Gaston 1991a, 1991b; Kangas 1992). However, we do know that it is being depleted at astonishing rates (Reid 1992; Whitmore and Sayer 1992; Myers 1993). Since the ratio of field biologists to species on this planet is very low, it is extremely unlikely that we will ever know enough about the particulars of the planet's biota to formulate a conservation strategy targeted to each taxon and region. We thus must attempt to make generalizations about the distribution of biodiversity and about how biodiversity might be evaluated when our evidence is limited.

The species-area curve holds much promise as a tool in conservation biology. The species-area curve has already played an important role in island biogeography theory (MacArthur and Wilson 1963, 1967; MacArthur 1965; Williamson 1981). To a large degree, the discipline of conservation biology emerged from this theory (Hoehne 1981; Harris 1984; Quinn and Hastings 1987; Quinn and Harrison 1988). One important example of how the species-area relationship has influenced conservation biology is the "single large or several small" (SLOSS) debate, which addressed the question about whether it is better to arrange a fixed amount of preserve area in a single large or several small preserves (Wright and Hubbell 1983; Soulé and Simberloff 1986; Blake and Karr 1987; Woolhouse 1987; Loman and von Schantz 1991). Although the debate has never been resolved per

se, it has moved on to more detailed issues such as the ideal arrangement of preserves, optimizing forestry practices, the presence of corridors, and buffer zones (Harris 1984; Noss and Harris 1986; Ehrenfeld and Schneider 1991; Harris and Atkins 1991; Noss 1991; Spellerberg 1991; Inglis and Underwood 1992). Even though SLOSS may not be debated any longer, its "descendents" still rely on the existence of a species-area relationship.

The results of this study indicate that although the species-area relationship can be quite complex, it does possess certain regularities. If this can be shown to be the case for much larger regions, there is much promise in applying the species-area curve to questions of preserve design.

The species-area curve has also been used in estimating species richness in large regions such as preserves (Evans et al. 1955; Williams 1964; Kilburn 1966; Lauga and Joachim 1987; Westfall et al. 1987; Gentil and Dauvin 1988; Gitay et al. 1991; Baltanás 1992; Grassle and Maciolek 1992). By fitting a function to the species-area curve, one could potentially extrapolate to an area much larger than the area sampled. However, it is clear from figures 2 and 4 that there is no such thing as *the* species-area curve for a given location. Rather, there is a suite of species-area curves, each with its own characteristics. In theory, all of the species-area curves for a given region should converge at two points: (area = 0, richness = 0) and (area = area of the entire region, richness = total richness of the region). We are very interested in estimating the latter point, because it represents the region's biodiversity. Unfortunately, the species-area curves in this study do not show any evidence of converging to the right into a single point (fig. 2). The envelopes for these curves (fig. 3) indicate a wide range of allowable species-area curves, even for a particular grain and extent; these curves may point in different directions. Thus it is misleading to use species-area curves to estimate the number of species in a large region. Studies on similar forests have shown that species-area curve methods tend to estimate species richness poorly (Kilburn 1966; Palmer 1990a).

Nevertheless, the fact that the species-area relationship can be decomposed into its components (figs. 2, 5, 9) is grounds for optimism: simple species-area models can potentially be improved to include some of the complexities of scale.

CONCLUSIONS

We have demonstrated that the positive relationship between species richness and area is influenced by grain, extent, and the number of samples in the Oosting Natural Area. Of these, grain is the most important. However, the species richness at a given area is determined by an interaction between the various components of scale. Despite this complexity, the species-area relationship exhibits marked regularities, which suggests fairly simple underlying causes. It remains to be demonstrated that such regularities exist at much larger grains and extents.

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