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COMMUNITY AREA AND FOOD-CHAIN LENGTH: THEORETICAL PREDICTIONS

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Abstract.—In combination with the simplest forms of the species-area curve (a power function or a simple proportionality between species and area), the cascade model predicts that the maximal chain length of a community food web (the height) should increase more slowly than linearly as a function of the logarithm of area and asymptotically in islands with extremely large area and extremely large numbers of species. The average chain length, according to the cascade model, should exceed 3.5 as soon as islands are large enough to have thirty or more species and should approach a finite limit, approximately 4.0, in webs from arbitrarily large islands. Thus the ratio of the height to the average chain length in the cascade model asymptotically increases without limit in webs from very large islands with very large numbers of species. According to the superlinear homogeneous model, both the height and the average chain length increase as a power, less than one, of the number of species, and therefore as a power, less than one, of area. The ratio of maximal to average chain length in the superlinear homogeneous model asymptotically approaches the limit e in webs from very large islands with very large numbers of species. The quantitative predicted length-area curves derived here are best tested by average food-chain lengths computed from observed complete food webs on islands of widely varying sizes, from small to large, in which other environmental factors such as productivity, environmental variability, and distance from a source of colonization do not vary notably. If the predicted area-height curves are to be tested with data from islands of small to moderate sizes, tailored simulations are recommended for obtaining the predicted distribution of height.

As the area of an island or the volume of any natural habitat increases, the diversity (measured by the number of species) of resident organisms usually increases. As the diversity of resident organisms increases, the length of the longest or average food chain involving those organisms is expected to increase. The purpose of this article is to compute theoretical length-area curves: testable, quantitative predictions about the increase of maximal or average food-chain length as a function of island area or habitat volume. These length-area curves are derived by splicing the species-area curve, one of the best-known quantitative empirical generalizations of ecology (see, e.g., MacArthur and Wilson 1967; Diamond and May 1981; Schoener 1986), with the relations between the numbers of species and the average or the maximal chain length given by two simple stochastic models of community food webs (one called the cascade model and one called the superlinear homogeneous model; Cohen 1990). The data required to test these predictions are not available now, but the publication of quantitative, testable length-area curves may spur the collection of the required data.

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In their simplest form, species-area curves assert that the number of biological species on an island is proportional to the area of the island raised to some power less than or equal to one, all else being held equal. When examined in detail (see, e.g., Connor and McCoy 1979; Sugihara 1981; Schoener 1986; Lomolino 1989), species-area curves are vastly more complicated and are influenced by the distance of islands from the source of colonization, the numbers of species in the source of colonization, the geological history of the islands, and the ecological roles of the species involved. As a first approximation, all these complications will be ignored.

The units of description in food webs, unlike species-area curves, are rarely biological species. Investigator-defined species are whatever categories the original report of a food web happened to use. These categories are sometimes broad (algae, phytoplankton, or land vegetation) and sometimes narrow (first instar larvae of a particular biological species of insect or fingerling fish of a particular biological species). Some investigators (e.g., Schoener 1989; Cohen et al. 1990) analyze food webs in terms of "trophic species." Ideally, a trophic species is an equivalence class of all organisms with identical sets of predators and identical sets of prey. In the analysis of real data, the diets and predators of each organism are not known; only the diets and predators of investigator-defined species are known. Therefore, operationally, a trophic species is an equivalence class of those investigator-defined species that have identical sets of predators and identical sets of prey.

Because of the difference in units of analysis, it will be necessary to convert from biological to trophic species in linking species-area curves and food-web models.

The cascade model (Cohen and Newman 1985) accounts for varied empirical observations about webs (Cohen et al. 1990). The model predicts, among other things, how the average and the maximal lengths of chains should depend on the number of trophic species in a community (Newman and Cohen 1986). According to Schoener (1989), the number of trophic species is approximately proportional to the 0.6805 power of the number of investigator-defined species, which were sometimes proper biological species, in his edited version of most of the webs in the Briand-Cohen collection. If the number of investigator-defined species is proportional to the number of biological species, a combination of a species-area curve, Schoener's power law, and the cascade model yields a testable prediction of how food-chain lengths should vary on islands of different areas. Other predictions are obtained by replacing the cascade model with variations of it such as the superlinear homogeneous model. All these predictions will be referred to as length-area curves.

Even without formulas, it is evident that, if the number of biological species on an island increases slowly with area, and if the number of trophic species increases linearly or less rapidly with the number of biological species, and if the maximal and the average chain length in a web increase very slowly with the number of trophic species in a community, then the maximal and the average chain length should increase extremely slowly with increasing island area. The balance of this article renders this conclusion quantitative.

FOOD-WEB DEFINITIONS AND ASSUMPTIONS

A web can be represented by a directed graph. Each vertex represents a trophic species, that is, a group of organisms that take the same kinds of prey and are eaten by the same kinds of predators. A trophic species is basal if it has no prey (that is, if it has no prey recorded in the web) and is top if it has no predators (recorded in the web). If trophic species A eats trophic species B, the web contains an arc, or trophic link, from B to A; the direction of the link indicates the direction of the flow of energy and materials. A chain is a sequence of links joined head-to-tail from a basal trophic species to a top trophic species. The length of a chain is the number of links it contains. The maximal chain length, or height, of a web is the largest of the chain lengths in a web. The average chain length is the average over all possible chains, with each chain weighted equally. If A is a basal species and B is a top species, there may be multiple chains of varying lengths from A to B; each such chain contributes equally toward the average chain length.

The height and the average chain length of a web are well-defined if the web has no cycles of any length. Since nearly all the webs in Cohen et al. (1990) are acyclic (except for cannibalism, which was simply suppressed), we shall assume that all webs are acyclic in the following theoretical calculations. Schoener (1989) has described a reasonable way of dealing with the rare cycles that occurred in his independent editing of most of the same webs analyzed in Cohen et al. (1990).

The cascade model and its extensions assume that all trophic species in a web may be numbered from 1 to S_T, with zero probability of a link from species i to species j unless $i < j$. The cascade model assumes that, if $i < j$, then the probability of a link from a trophic species numbered i to a trophic species numbered j is

$$p = c/S_T . \tag{1}$$

The best current estimate of c, the sole parameter of the cascade model, is 4.0, the value that will be used in numerical calculations here (Cohen 1990). When $c = 4.0$, the predicted average number of trophic links is approximately twice the number of trophic species in webs with a moderate to large number of species. (Here is the calculation: $E(L)$, the expected number of trophic links, is given by $E(L) = pS_T(S_T - 1)/2$, and with p given by eq. [1] and $c = 4.0$ it follows that $\lim_{S_T \to \infty} E(L)/S_T = 2.0$.) This prediction is consistent with observations of webs that have 3–48 trophic species, which is a rather limited range of variation of S_T (Cohen et al. 1986). The cascade model is meaningful only for values of S_T larger than c, since c/S_T is assumed to be a probability less than one.

An alternative to equation (1), favored by Schoener (1989), and considered elsewhere at Schoener's suggestion (Cohen 1990), is that

$$p = 1.38 S_T^{0.35}/(S_T - 1) \approx 1.38 S_T^{-0.65} , \tag{2}$$

so that $E(L)$ increases superlinearly with the number of trophic species according to the equation $E(L) = pS_T(S_T - 1)/2 = 0.69 S_T^{1.35}$. This power-law estimated relation between the number of trophic species, S_T, and $E(L)$ is obtained by nonlinear least squares from data on 113 food webs (Cohen 1990). The model

TABLE 1

RANGE OF PARAMETERS OF THE POWER FUNCTION AND UNTRANSFORMED SPECIES-AREA CURVES IN 100 SETS OF SPECIES-AREA DATA

	INTERCEPT		SLOPE	
MODEL	Low	High	Low	High
Species as function of area	−23.7	1,626.3	−.001	2,645.1
Log species as function of log area	−4.40	3.70	−.276	1.13

SOURCE.—Values are extracted from table 2A of Connor and McCoy (1979, pp. 824–826).

obtained from the cascade model by assuming equation (2) instead of equation (1) is referred to as the superlinear homogeneous model (Cohen 1990).

The number of trophic links per species is constant in the cascade model but increases with increasing numbers of species in the superlinear homogeneous model. For 21 trophic species, both models give approximately two trophic links per trophic species. For more than 21 trophic species, the superlinear homogeneous model gives more than two links per species.

The cascade and superlinear homogeneous models make no allowance for spatial heterogeneity. When these models are spliced to a species-area curve, they assume that each potential species of prey is equally accessible to each potential species of predator (R. D. Holt, personal communication), regardless of location, even in the limit as the size of an island gets large. This assumption may be reasonable if all species have access to all others throughout an island but seems less plausible if an island contains diverse habitats such as ponds, rivers, forests, and grasslands. It is an empirical question, to be decided by future fieldwork, whether the cascade and superlinear homogeneous models apply only to webs from local communities in more or less homogeneous habitats, like most of the empirical webs the models were intended to describe, or whether the models also can describe webs from large, physiographically diverse islands.

SPECIES-AREA DEFINITIONS AND ASSUMPTIONS

Connor and McCoy assembled 100 sets of species-area data and fitted four linear regressions to each: log species as a function of log area (the so-called power function); species as a function of area (the so-called untransformed relation); log species as a function of area (the exponential relation); and species as a function of log area (the logarithmic relation). (Area was measured in square kilometers.) Connor and McCoy stated: "Of the 4 linear models we examined, the power function and the untransformed models provide good fits most frequently." The linear regressions were often far from a tight description of the data. In five of the 100 cases the linear correlation between species and area was even negative. In some instances, the logarithmic relation proved superior. Notwithstanding its reputation as an ecological "law," the species-area curve (of whatever form) is a considerable idealization of the data. Table 1 shows the range of variation in the intercepts and slopes of the regressions of log species on log area and of species on area. Since the range of intercepts for the untransformed relation contains zero, it does no violence to the data to take the intercept as zero and thus take the untransformed relation as a simple proportionality between species and area. (While an island with no area can contain no species, an island with no species may have positive area, because a minimum area may be required for species to invade; however, table 1 does not demonstrate that such a minimum area, if it exists, is greater than zero.)

We now define some notation needed to state the power function and untransformed relations mathematically. Let A denote the area of an island, lake, or other bounded habitat. Let $S_{\mathrm{B}}(A)$ denote the number of biological species counted on that island. The power law is

$$S_{\mathrm{B}}(A) = kA^{z}, \tag{3}$$

where k is a proportionality constant and z is a positive constant (ordinarily) less than one. (We shall pass over the rarely recognized problem of interpreting the dimensionality of k when $z < 1$.) In numerical computations, we take $z = 1/4$ and $k = 1$ in equation (3). The actual value of k depends on the units used to measure area, and no information about the shape of the relation between area and average chain length is lost by taking $k = 1$. The values $z = 1/4$ and $k = 1$ fall nicely within the ranges found by Connor and McCoy (1979) and shown in table 1.

The species that appear in species-area curves typically are drawn from much narrower taxonomic units than the species that appear in food webs. For example, species-area curves are often restricted to birds, mammals, insects, or plants. Within such restricted sets of species, feeding relations may be reduced or absent. An attractive feature of the power law is that it is additive for different kinds of species (birds, mammals, insects, and plants) so long as the exponent z is the same for each different kind (T. W. Schoener, personal communication). This important feature makes it valid to apply the power law to all the kinds of species found in food webs, provided z is the same for all kinds.

The untransformed or linear species-area function is obtained from equation (3) by setting $z = 1$ and taking k (usually) to be positive. Of course, k depends on the units used to measure A.

We assume that the number of trophic species is a power function of the number of biological species, that is, for some positive exponent y, that

$$S_{\mathrm{T}} = KS_{\mathrm{B}}^{y}, \tag{4}$$

where K is a positive constant. If $y = 1$, then the number of trophic species is directly proportional to the number of biological species. In an earlier article (Cohen and Newman 1988), we offered theoretical arguments to justify this proportionality; for simplicity, we took $K = 1$. In a regression of log (trophic species) as a function of log (investigator-defined species), Schoener (1989) estimates that $y \approx 0.6805$ and $K \approx 1.7793$ (T. W. Schoener, personal communication). In the sections Maximal Chain Lengths and Average Chain Lengths, both forms of equation (4) are compared.

Figure 1 compares the two different forms of equation (4) for biological species in the range from 10 to 70. Small numbers of species are omitted from figure 1,

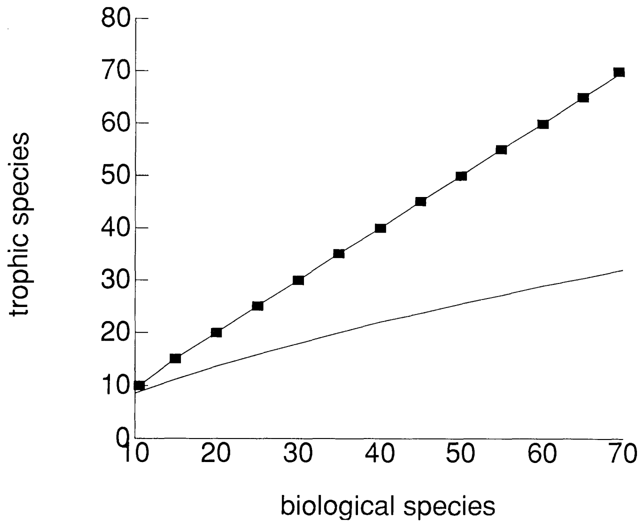

FIG. 1.—Number of trophic species as a function of the number of biological or investigator-defined species. *Upper curve,* function when trophic species are assumed to equal biological species (Cohen and Newman [1988] relation). *Lower curve,* function when $K = 1.7793$ and $y = 0.6805$ in eq. (4) (Schoener [1989] power law).

and small island areas are omitted from figure 2 and figure 3, for empirical and theoretical reasons. Empirically, webs with small numbers of species are probably poor samples of natural communities, except for extremely small or depauperate habitats. Theoretically, the calculations for large numbers of species do not apply to islands too small to contain large numbers of species.

Substituting equation (3) into the right side of equation (4) gives a predicted relation between the area of an island and the number of its trophic species:

$$S_{\mathrm{T}} = Kk^{y}A^{yz}. \qquad (5)$$

Obviously, if $y < 1$, as Schoener (1989) finds, the number of trophic species will increase more slowly with increasing island area than the conventional species-area curve predicts for the number of biological species.

MAXIMAL CHAIN LENGTHS

This section deals with the height, or the maximal chain length; the next with the average chain length. In this section, the numbers of species are assumed to be so large that we can use the asymptotic theory of height for the cascade model (Newman and Cohen 1986) and the superlinear homogeneous model (C. M. Newman, unpublished manuscript). This case is tractable mathematically but is probably unrealistic biologically. In the next section, more realistically, we do exact numerical calculations for finite numbers of species as well as asymptotic calculations for very large numbers of species. In both sections, we analyze first the cascade model, then the superlinear homogeneous model.

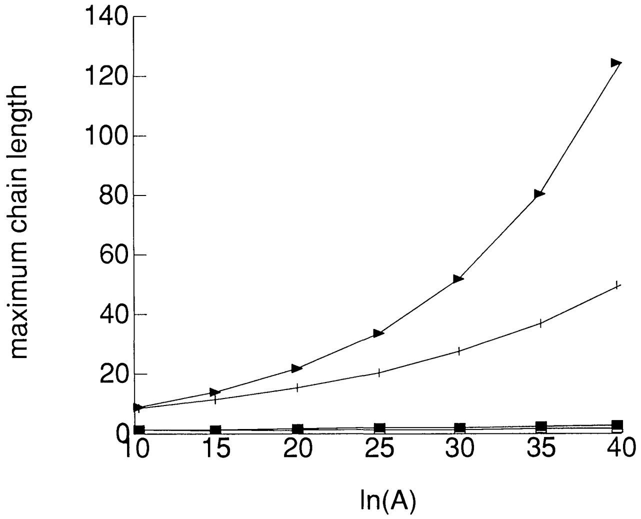

FIG. 2.—Height, or maximal chain length, as a function of the natural logarithm of area for very large islands, as predicted by various models and the species-area power law. Parameters: $c = 4.0$ in the cascade model; $k = 1$ and $z = 1/4$ in the species-area curve. *Filled squares,* cascade model ($c = 4.0$) with trophic species equal to biological species; *empty squares,* cascade model ($c = 4.0$) with $K = 1.7793$ and $y = 0.6805$ in eq. (4); *filled triangles,* superlinear homogeneous model with trophic species equal to biological species; *vertical lines,* superlinear homogeneous model with $K = 1.7793$ and $y = 0.6805$ in eq. (4).

Let H be the height of a web with S_T trophic species. Then, according to the cascade model (Newman and Cohen 1986, p. 369), when S_T becomes very large, the ratio of H to $\ln(S_T)/\ln[\ln(S_T)]$ is arbitrarily close to one with a probability that approaches one. We write this relation as

$$H \sim \frac{\ln(S_T)}{\ln[\ln(S_T)]} \quad \text{as } S_T \to \infty . \tag{6}$$

(This does not imply that the difference between H and $\ln(S_T)/\ln[\ln(S_T)]$ is arbitrarily small with high probability, because H and $\ln(S_T)/\ln[\ln(S_T)]$ could differ by an amount that goes to infinity more slowly than $\ln(S_T)/\ln[\ln(S_T)]$.) Elsewhere, we give higher-order correction terms for the asymptotic expansion (6) (Newman and Cohen 1986).

According to the superlinear homogeneous model (C. M. Newman, unpublished manuscript), when S_T becomes very large, the ratio between H and epS_T is arbitrarily close to one, where p is given by equation (2), with a probability that approaches one. We write this relation in numerical form as

$$H \sim 3.751\, S_T^{0.35} \quad \text{as } S_T \to \infty . \tag{7}$$

Higher-order correction terms to asymptotic expansion (7) are given by C. M. Newman (unpublished manuscript).

The height-area curve for the cascade model is obtained by substituting equation (5) into asymptotic expansion (6):

$$H \sim \frac{yz\ln(A)}{\ln[\ln(A)]} \quad \text{as } A \to \infty . \tag{8}$$

The height predicted by the cascade model grows very slowly with increasing area, A (fig. 2), less than linearly in a plot of height as a function of the logarithm of area, as the area becomes extremely large. The asymptotic behavior of H is independent of the proportionality constant k in equation (3) and of the proportionality constant K in equation (4).

The height-area curve for the superlinear homogeneous model is obtained by substituting equation (5) into asymptotic expansion (7):

$$H \sim CA^{0.35yz} \quad \text{as } A \to \infty , \tag{9}$$

and

$$C \approx 1.38e(Kk^{y})^{0.35} ,$$

where $yz \leq 1$ (since $y = 0.6805$ or $y = 1$, and $z = 1/4$ or $z = 1$). As the area becomes extremely large, the height predicted by the superlinear homogeneous model grows exponentially as a function of the logarithm of area (fig. 2); as a function of area directly, the height grows very slowly because, since $yz \leq 1$, the exponent $0.35yz$ in asymptotic expansion (9) cannot exceed 0.35.

AVERAGE CHAIN LENGTHS

The average chain length, $M(S_T)$, in a model web with S_T species and a given probability p of a link from species i to species j, where $i < j$, is the same for both the cascade model and the superlinear homogeneous model (Newman and Cohen 1986, p. 358):

$$M(S_T) = S_T p \frac{(1+p)^{S_T - 1} - (1-p)^{S_T - 1}}{(1+p)^{S_T} - (1-p)^{S_T} - 2S_T p(1-p)^{S_T - 1}} . \tag{10}$$

Under the cascade model's assumption (eq. [1]) about p, this simplifies slightly to

$$M(S_T) = \frac{c\left[\dfrac{S_T}{S_T + c} - R^{S_T}\left(\dfrac{S_T}{S_T - c}\right)\right]}{1 - R^{S_T}\left[1 + 2c\left(\dfrac{S_T}{S_T - c}\right)\right]} , \tag{11}$$

where $R = (S_T - c)/(S_T + c)$ for $S_T > c$ and the average chain length approaches a finite limit as the number of trophic species increases indefinitely:

$$\lim_{S_T \to \infty} M(S_T) = \frac{c(1 - e^{-2c})}{1 - e^{-2c}(1 + 2c)} , \tag{12}$$

which is approximately 4.01 if $c = 4.0$. This limit is independent of the parameters k and z in equation (3) and is approached fairly rapidly. For example, the average chain length is predicted to exceed 3.5 as soon as islands are large enough to have 30 or more trophic species; if $S_T = 100$, $M(100) = 3.86$.

Comparing asymptotic expansion (6) and equation (12) shows that the ratio of the height to the average chain length in the cascade model increases without limit as the number of trophic species gets large. Intuitively, there might be two possible reasons for this phenomenon. First, the tail of the distribution of chain lengths could get fatter as the number of trophic species gets larger. Second, and alternatively, as the number of trophic species gets larger, an increasing number of chains might be sampled from a fixed distribution of chain lengths, so that very long chains, with a fixed low probability, would be more likely to be observed. In fact, the second possibility is true and the first is not; the expected number of chains of any given length, divided by the expected number of all chains, approaches a positive constant as the number of trophic species gets large (Newman and Cohen 1986).

Under the superlinear homogeneous model's assumption in equation (2), equation (10) does not simplify appreciably for finite S_T. But as S_T increases without limit, the ratio of the average chain length to $S_T p$ approaches one, that is,

$$M(S_T) \sim S_T p = 1.38 S_T^{0.35} . \tag{13}$$

To see asymptotic expansion (13), divide the numerator and denominator of equation (10) by $(1 + p)^{S_T - 1}$ and note that

$$\left(\frac{1-p}{1+p}\right)^{S_T - 1} \leq (1 - p)^{S_T - 1} \leq e^{-p(S_T - 1)} = e^{-1.38(S_T - 1)/S_T^{0.65}} \sim e^{-1.38 S_T^{1-0.65}} \rightarrow 0 ,$$

so that

$$M(S_T) = \frac{1.38 S_T^{0.35}}{1 + 1.38 S_T^{-0.65}} + O(e^{-\epsilon S_T^{0.35}})$$

for any positive constant, $\epsilon > 0$, which is a more precise version of asymptotic expansion (13). Here O is the usual symbol for order of magnitude.

Comparing asymptotic expansion (7) and equation (13) shows that the ratio of the height to the average chain length in the superlinear homogeneous model approaches the limit e as the number of trophic species gets large. Thus there is a qualitative difference in the ratio of the height to the average chain length between the cascade and the superlinear homogeneous models.

In webs with finite numbers of trophic species, Schoener (1989) finds empirically that the height and the average chain length are very closely correlated. If the numbers of trophic species in these webs were large enough for the asymptotic theory described here to apply, then the close correlation between the height and the average chain length would provide evidence for the superlinear homogeneous model and against the cascade model. However, a simulation study is needed to compare the correlation between maximal and average chain lengths in the two models, in webs with the numbers of trophic species actually observed, before it can be concluded that Schoener's observed correlation favors one model or the other.

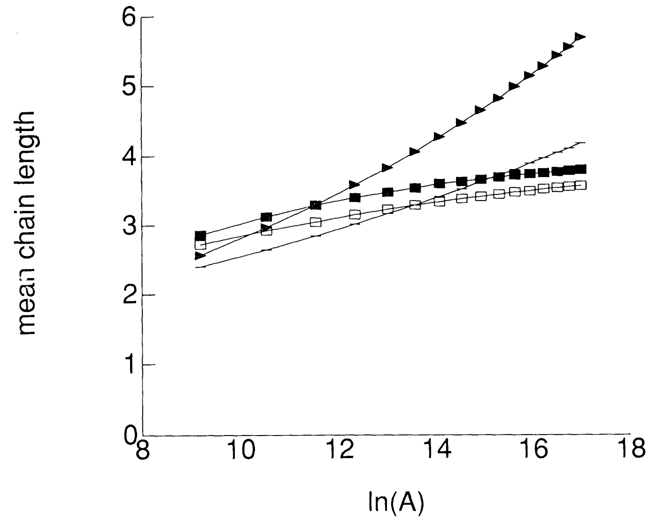

FIG. 3.—Average chain length as a function of the natural logarithm of island area predicted by various models and the species-area power law. Parameters: $c = 4.0$ in the cascade model; $k = 1$ and $z = 1/4$ in the species-area curve. *Filled squares,* cascade model ($c = 4.0$) with trophic species equal to biological species; *empty squares,* cascade model ($c = 4.0$) with $K = 1.7793$ and $y = 0.6805$ in eq. (4); *filled triangles,* superlinear homogeneous model with trophic species equal to biological species; *horizontal lines,* superlinear homogeneous model with $K = 1.7793$ and $y = 0.6805$ in eq. (4).

Figure 3 shows the relations between area and average chain lengths for a range of areas corresponding to 10–70 biological species according to equation (3) with $k = 1$, $z = 1/4$. Whereas the average chain lengths approach a limit in the cascade model, they increase exponentially with the increasing logarithm of the area (i.e., as a positive power of area) in the superlinear homogeneous model, as guaranteed by the combination of asymptotic expansion (13) and equation (5). It would be highly desirable to have data capable of distinguishing between the predictions of the cascade and the superlinear homogeneous models.

RELATED PRIOR STUDIES

There have been many prior theoretical and empirical attempts to relate the length of food chains to environmental factors (see, e.g., for recent reviews, Pimm 1982; Yodzis 1984, 1989; Schoener 1989; Cohen et al. 1990). Schoener's (1989, p. 1568) "productive space hypothesis" is related to the theory developed here. Schoener defines productive space as space (area or volume) times productivity. The productive-space hypothesis asserts that the height of a web is "determined by the amount of productive space required to allow critical component species populations to persist with some high probability. . . . The productive space hypothesis implies th[a]t maximum food-chain lengths should be greater, the greater the quantity: area (or volume) occupied by the food web times the productivity of that web."

Qualitatively, the productive-space hypothesis is consistent with Schoener's (1989, p. 1560) observations of the Bahamian archipelago. On middle-sized islands, a "typical" web has medium-size carnivores, small carnivores, small herbivores, and producers. The largest islands also have large carnivores, while the smallest islands lack medium and sometimes small carnivores. Consequently, "when the major elements alone are used as trophic species" (Schoener 1989, p. 1567), the largest islands have a height of three to four, medium-size islands have a height of two to three, smaller islands have a height of two, and the smallest islands have a height of one or even zero. The biological rationale is that "larger animals, and particularly larger carnivores, are less likely to occur on smaller islands" (Schoener 1989, p. 1567).

Schoener (1989, pp. 1570–1571) observes: "The productive space hypothesis is difficult to evaluate directly for most webs, as even fewer studies provide figures on the area or volume occupied by the web as on productivity. . . . More precise testing will necessitate the difficult task of measuring areas or volumes that particular food webs occupy."

FIELD-TESTING THE PREDICTIONS

The length-area curves in this article may be viewed as one (not the only) possible quantitative specification of Schoener's productive-space hypothesis, in the special case that the productivity of different islands is constant. When productivity is constant across islands, Schoener's productive-space hypothesis asserts that web height should depend on island size. The length-area curves given here, which were developed independently of Schoener's productive-space hypothesis, predict quantitatively how height should depend on island size, for large islands, and also predict quantitatively how average chain length should depend on island size for islands of all sizes.

Empirical tests of these predictions should hold constant, to the extent possible, all environmental factors other than area. Other factors that could confound a test of these predictions include productivity, distance from a source of colonization, and environmental variability. Clearly islands with extremely low productivity, no matter how large, will be unable to support food chains as long as those on smaller, highly productive islands. (Similarly, empirical tests of Schoener's productive-space hypothesis would need to hold constant all factors other than area or volume and productivity, such as distance from a source of colonization and environmental variability.)

The average chain length is a stabler statistic than the height. (This means that in different replications of a food web with a given number of species and a given probability of a trophic link, the height would be expected to vary considerably more than the average chain length.) Therefore it is desirable to test predictions concerning the average chain length before testing the height-area curves. Moreover, observed average chain lengths can be compared with predictions for both small and large islands, while the predicted heights are derived only for very large islands. To obtain the statistical stability offered by the average chain length, the field investigator will have to pay the price of gathering a complete food web, rather than looking only for the longest chain. Of course, a complete web can be used for many other purposes.

There are two problems in using very small islands (whether natural, such as those in the Bahamas, metaphorical, such as phytotelmata, or artificial, as in container experiments) to test the predicted length-area curves. First, the simple formula, equation (3), of the species-area curve conceals much scatter; it predicts with considerable relative error the actual number of species for very small islands. Second, the asymptotic calculations of height do not apply when the number of species is anything but very large. In the cascade model, while the height has a one-point or two-point distribution in the limit of a large number of species, simulations with a thousand species show that the height varies over a substantial range, and that range does not even include the value of the height given by the asymptotic formula (Newman and Cohen 1986).

For these reasons, if food webs can be determined for very small islands, it would probably be best to compare the observed heights and average chain lengths with simulations of the food-web models tailored to the data in hand, that is, with the same number of trophic species as observed and perhaps even the same probability, p, of occurrence of links as observed. If the observed number of links is L' and S_T is the observed number of trophic species, the edge probability, p, is estimated as $p' = L'/[S_T(S_T - 1)/2]$, which is identical to connectance, according to one definition. When p is estimated in this way, there is no difference between the cascade and the superlinear homogeneous models, so only one set of simulations need be performed. Simulation of these models is very simple: take an $S_T \times S_T$ matrix with all elements zero; independently for each element lying above the main diagonal replace zero with one with probability p (determined from eq. [1], eq. [2], or the estimation formula p' just given) and leave the zero as is with probability $1 - p$ (this completes the predation matrix of the simulated web); calculate the distribution of chain lengths (using, e.g., the efficient algorithm given in Cohen et al. [1986] and Cohen et al. [1990]); derive the average and the maximal chain lengths.

The length-area curves derived here rest on many simplifying assumptions, in addition to those implied separately by the species-area curve and the web models. For example, links between species are assumed to be determined independently, and with a different probability, in webs with different numbers of species, even when some of the same species may be present on different islands (R. D. Holt, personal communication). This assumption could be relaxed in various more complex models. Before such models are developed, however, it seems desirable to have at least some data to test the available simple predictions.

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