Eagle's medium supplemented with fetal bovine serum (10%). Subconfluent cells were transfected with pcDNA3–HA-MAPK and additional DNAs (*15*) by the DEAE-dextran technique. The total amount of plasmid DNA was adjusted to 3 to 4 μg per plate with vector DNA (pcDNA3; Invitrogen) when necessary; 2 days later, transfected COS-7 cells were cultured overnight in serum-free medium. Cells were then left untreated or were stimulated with various agents, washed in cold phosphate-buffered saline (PBS), and lysed at 4°C in a buffer containing 20 mM Hepes (pH 7.5), 10 mM EGTA, 40 mM β-glycerophosphate, 1% NP-40, 2.5 mM $MgCl_2$, 1 mM dithiotreitol, 2 mM sodium vanadate, 1 mM phenylmethylsulfonylfluoride, aprotinin (20 μg/ml), and leupeptin (20 μg/ml). The lysate was centrifuged at 14,000*g* for 20 min at 4°C, and proteins were immunoprecipitated and assayed for kinase activity. Equivalent expression of cDNA constructs was verified with the respective antibodies.

19. For the MAPK assay, after centrifugation, proteins from clarified supernatants were immunoprecipitated with monoclonal antibody (mAb) to hemagglutinin 12CA5 (Babco, Berkeley, CA) for 1 hour at 4°C, and immunocomplexes were recovered with Gamma-bind G (Pharmacia). Bound proteins were washed three times with PBS supplemented with 1% NP-40 and 2 mM sodium vanadate, once with 0.5 M LiCl in 100 mM tris (pH 7.5), and once with kinase reaction buffer [10 mM Mops (pH 7.5), 12.5 mM β-glycerophosphate, 7.5 mM $MgCl_2$, 0.5 mM EGTA, 0.5 mM sodium fluoride, and 0.5 mM vanadate]. Reactions were done in 30-μl volumes of kinase reaction buffer containing 1 μCi of [γ-^{32}P] adenosine triphosphate (ATP) per reaction, 20 μM unlabeled ATP, and myelin basic protein (MBP) (1.5 mg/ml) (Sigma) at 30°C for 30 min. Reactions were terminated by addition of 5× Laemmli buffer. Samples were boiled and proteins were separated by SDS–polyacrylamide gel electrophoresis (PAGE) (12% gel). Phosphorylated MBP was visualized by autoradiography and quantified with either a phosphorimager or a liquid scintillation detector. Parallel samples were immunoprecipitated with antibody to HA and processed for protein immunoblot analysis with a MAPK-specific antiserum.
20. Lysates of total cellular protein or anti-HA immunoprecipitates were analyzed by protein immunoblotting after SDS-PAGE with the corresponding rabbit antiserum or mouse mAb. Immunocomplexes were visualized by enhanced chemiluminescence detection (Amersham) with the use of goat antiserum to rabbit or mouse immunoglobulin G coupled to horseradish peroxidase (Cappel, West Chester, PA). Mouse mAbs to the HA epitope 12CA5 were purchased from Babco. Rabbit polyclonal antisera to c-Src, Shc, and Grb2 were purchased from Santa Cruz Laboratories (Santa Cruz, CA) or Upstate Biotechnology (Lake Placid, NY).
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Uniting Two General Patterns in the Distribution of Species

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Two patterns in the distribution of species have become firmly but independently established in ecology: the species-area curve, which describes how rapidly the number of species increases with area, and the positive relation between species' geographical distribution and average local abundance. There is no generally agreed explanation of either pattern, but for both the two main hypotheses are essentially the same: divergence of species along the ecological specialist-generalist continuum and colonization-extinction dynamics. A model is described that merges the two mechanisms, predicts both patterns, and thereby shows how the two general, but formerly disconnected, patterns are interrelated.

The species-area (SA) curve is one of the few universally accepted generalizations in community ecology (*1–3*), but ecologists have failed to agree on the mechanisms that produce this pattern (*3*). According to the habitat heterogeneity hypothesis, large areas have more species than small ones because of their greater range of distinct resources, which facilitates the occurrence of ecological specialists (*3*). As an alternative, MacArthur and Wilson (*2*) advanced the dynamic theory of island biogeography, which predicts that species richness increases with area owing to decreasing extinction rate with increasing area.

Another general pattern in the distribution of species has been well documented only during the past 15 years (*4, 5*): species with wide distributions tend to be locally more abundant than species with narrow distributions. We call this relation the distribution-abundance (DA) curve. The two most widely recognized explanations of the DA curve are Brown's niche breadth hypothesis and metapopulation dynamics. According to Brown's hypothesis (*5*), generalist species, or species using ubiquitous resources (*6*), are both locally common and widely distributed, whereas specialists are constrained to have narrow distribution and tend to be locally uncommon. Metapopulation dynamic models predict that locally common species become widely distributed because of their low extinction rates and high colonization rates (*7, 8*). High migration rates from existing large populations may additionally "rescue" small populations from extinction, in which case a wide distribution with many large populations tends to enhance average local abundance (*7*).

Surprisingly, although the two main hypotheses about the SA and DA curves are strikingly similar, the two patterns themselves have been studied without any reference to each other (*9*). To bring conceptual unity to this area of ecology, we demonstrate that the SA and DA curves are both predicted by the same model, which furthermore merges the two "competing" hypotheses, namely, ecological specialization (habitat heterogeneity) and extinction-colonization dynamics.

To construct the model, consider a set of *R* islands (*10*) populated by a "pool" of *Q* species. The islands differ in area; we denote by m_A and $\sigma_A{}^2$ the mean and the variance of the logarithm of island areas (base *e* is used throughout this report). Likewise, the species differ in their abundances per unit area (density), with m_w and $\sigma_w{}^2$ denoting the mean and the variance of the logarithm of species densities (*11*). By definition, the "carrying capacity" (equilibrium population size) of species *i* on island *j* is given by $K_{ij} = w_i A_j$, where w_i is the density of species *i* and A_j is the area of island *j*.

Following the standard approach to modeling metapopulation dynamics (*7*), we model changes in the probability $p_{ij}(t)$ of species *i* being present on island *j* at time *t*, in the absence of interspecific interactions, as

$$\frac{dp_{ij}}{dt} = C_i(t)[1 - p_{ij}] - \mu_{ij}p_{ij} \qquad (1)$$

where $C_i(t)$ is the colonization rate of empty islands and μ_{ij} is the extinction rate of extant populations. Empirical studies suggest that μ_{ij} is roughly proportional to $1/K_{ij}$ (*12, 13*), and we use this approximation below. The appropriate expression for $C_i(t)$ is different for two fundamentally different scenarios. In a mainland-island situation, the presence of species on islands is dependent on colonization from a permanent mainland community, where the density of species *i* is w_i. In this case, $C_i(t)$ is given by cw_i, where the value of parameter *c* decreases with increasing distance to the mainland. In contrast, in the classical metapopulation there is no external mainland, and the empty islands are colonized from other occupied islands (*7, 14*). Here it is reasonable to assume that the colonization rate of empty islands is proportional

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to the pooled abundance of the species in the network of islands, and hence $C_i(t) = cw_i\Sigma p_{ij}(t)A_j$.

We focus in our analysis on the equilibrium value of $p_{ij}(t)$, which is called the incidence of species *i* on island *j*, J_{ij} (*15*). The SA and DA curves are related to each other, because both curves are obtained by summing up the same set of incidences, but over different indices. The sum of the incidences across species gives the expected number of species on island *j*, S_j, whereas the sum of the incidences across islands gives the expected geographical distribution of species *i*, D_i. In the metapopulation literature, distribution is typically measured by the fraction of occupied islands, $P_i = D_i/R$ (*7*).

The most widely used statistical (descriptive) model of the SA curve is the power function model (*1–3*, *16*), $S = kA^z$, which is generally used in the log-transformed form (*3*),

$$\log S = \log k + z \log A$$

This model has the obvious drawback of being unbounded, contrary to common sense and empirical results (*13*, *17*). However, ecologists have found that the logarithm of species number (log S) generally increases roughly linearly with the logarithm of island area (log A) for a large range of island areas (Fig. 1, A and B). Empirical studies typically report the slope of the linear regression line, *z*.

The DA curve lacks a similar widely used statistical model. Here the empirical studies have been concerned with the demonstration that some sort of positive relation exists (*4*, *5*). Considering a mainland-island situation, the rarest species on the mainland often do not occur on any of the islands ($P = 0$), whereas the commonest species are found on all ($P = 1$) or most islands. This observation suggests a logistic model for the DA curve, with *P* increasing from zero to 1 with increasing density, *w*, or, as we will assume here, with increasing logarithm of density, log *w*:

$$P = \frac{1}{1 + e^{-a-b\log w}}$$

where *a* and *b* are two parameters. The logistic model can be linearized with the logit-transformation (*18*) (Fig. 1, C and D).

We are now ready to examine the model-predicted SA and DA curves. For the mainland-island situation, we have derived exact mathematical formulas for the slopes of the SA and DA curves (*19*). The predicted SA curve is approximately linear for several orders of magnitude of island areas (Fig. 1E). The slope of the curve is a function of two parameters, σ_w and *cA* (*19*), which can be estimated with empirical data (*20*). The parameter combination cA, and therefore the value of the slope, is a function of the ratio of colonization to extinction probabilities (*13*, *21*). The slope of the model-predicted DA curve is also approximately linear for a large range of species' densities (Fig. 1G), and it depends on three parameters: the mean (m_A) and the variance (σ_A) of island areas, and the parameter combination cw_i^2 (*19*).

For classical metapopulations without an external mainland, the slopes of the SA and DA curves can be calculated numerically (*15*). The model generates approximately linear SA and DA curves (Fig. 1, F and H), comparable to the respective curves for the mainland-island situation (Fig. 1E and G), except that the DA curve now has a vertical asymptote for small values of *w* (*22*) owing to an extinction threshold in classical metapopulation models (*7*).

Comparison of the mainland-island and metapopulation models (Fig. 2A) yields distinctly smaller SA slopes for the metapopulation model for comparable parameter values. In contrast, the DA curve is expected to be steeper for classical metapopulations than for mainland-island systems (Figs. 1, G and H, and 3, B and D) owing to the low vertical asymptote in the former.

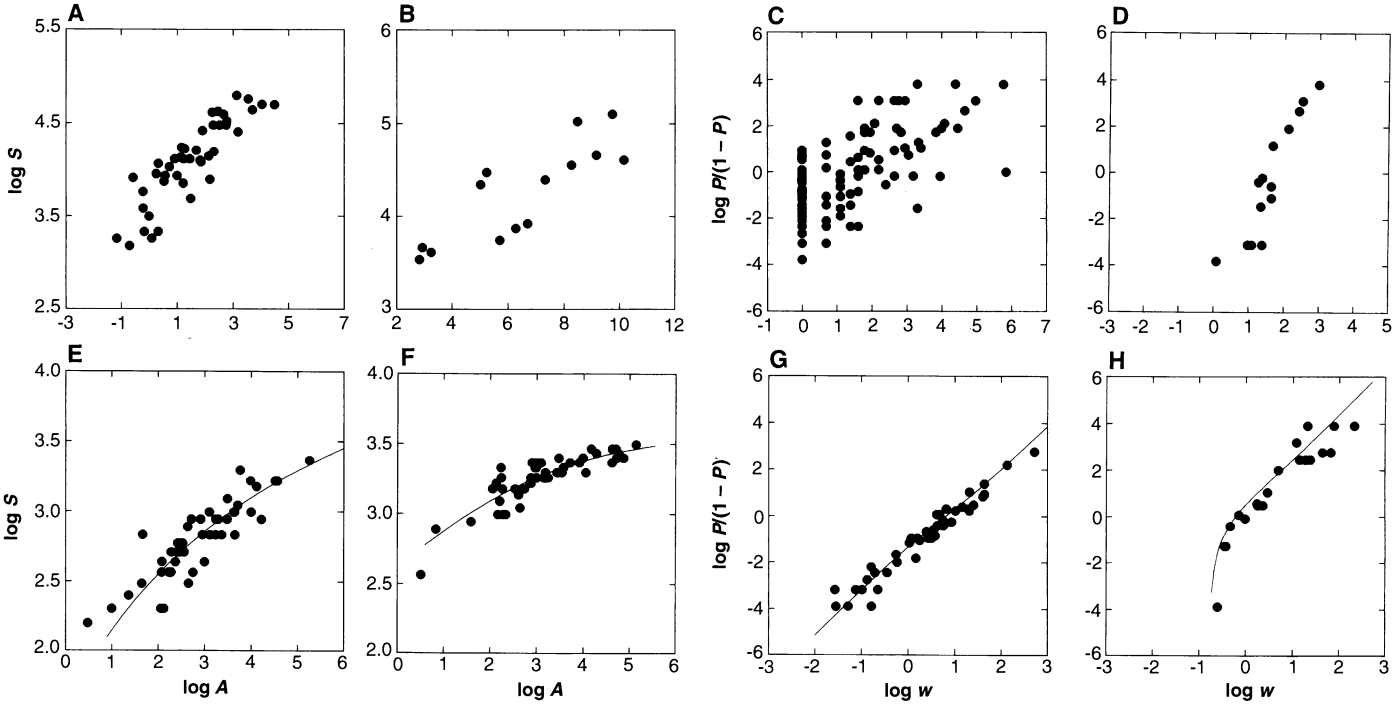

Fig. 1. Empirical and theoretical examples of approximately linear SA and DA curves. (**A** and **B**) The logarithm (base *e*) of species number against the logarithm of island area for (A) moths in a mainland-island system (*28*) and (B) birds in a metapopulation system (*29*). (**C** and **D**) The respective DA curves, with the logarithm of *P*/(1 − *P*) plotted against the logarithm of *w* (*18*). The slope values and their standard errors (in parentheses) are (A) 0.29 (0.02), (B) 0.18 (0.03), (C) 0.83 (0.09), and (D) 3.16 (0.40). (**E** to **H**) Corresponding model-predicted results, in which the continuous lines give the expected values (*19*), and the dots give a stochastic realization obtained by assigning species to a set of 50 islands with their predicted incidences on these islands (*15*). The following parameter values were used in all cases: $Q = 50$, $m_A = 3$, $\sigma_A = 1$, and $\sigma_w = 1.5$. To have comparable species numbers on the islands in the mainland-island and metapopulation models, we used the values of $c = 0.01$ in the former and $c = 0.00005$ in the latter, respectively.

Despite its simplicity, the model makes several quantitative predictions. First, it predicts the slopes of the SA and DA curves on the basis of measurable ecological parameters: the moments of the species abundance and island area distributions, and species' incidences on islands (Fig. 3). Parameter values that allow 20 to 80% of the species in the species pool to occur on an average-sized island generate *z* values ranging from 0.1 to 0.45 (Fig. 2A), which is the typical range of empirical values (Fig. 2B) (*2*, *3*). The model predicts that *z* increases with isolation, which is observed in empirical data (*2*, *3*) (for exceptions, see below), and that *z* decreases with increasing variance of the species abundance distribution (Fig. 3, A and C) (*19*).

Second, the model accounts for the empirically observed small *z* values on mainlands (Fig. 2B) (*2*, *3*) without resorting to an ad hoc assumption about "transient" species inflating the species number in small study areas (*3*). In contrast, in the present model the small *z* values on mainland are due to the lack of rare species in the largest study areas; rare species go extinct from the entire network (Figs. 1H and 3D).

Third, the model explains the apparent exception of small *z* values in some very isolated archipelagoes (*13*). The *z* value is predicted to be large for isolated islands if colonization occurs from the mainland, but small if colonization occurs among the islands, which may well happen in the most isolated archipelagoes.

Fourth, the model demonstrates that the exact shape of the species abundance distribution is not critical for realistic SA curves and *z* values (*23*), contrary to the suggestions of phenomenological (sampling) models based on the canonical lognormal species abundance distribution (*24*). What is critical is that there are some interspecific differences in abundance; previous dynamic models that ignored interspecific differences failed to predict realistic SA curves without making the implausible assumption of complete density compensation among competing species (*13*, *25*). Furthermore, interspecific differences in abundance must generate differences in species' distributions, as happens mechanistically in the present model. In contrast, the assumption by previous models of a random or nonrandom but fixed distribution of individuals in space (*26*) does not generate realistic SA curves and entirely fails to predict the effect of isolation on *z*.

In summary, not only can the SA and DA curves be predicted by the same model, the DA curve appears also to be a necessary ingredient of realistic SA curves. The model also predicts another widespread property of island communities, the nested-subset distribution of species on islands and habitat islands (*27*). One open question that remains is to what extent the present results, based on a model of regional dynamics, can be extended to a continental scale.

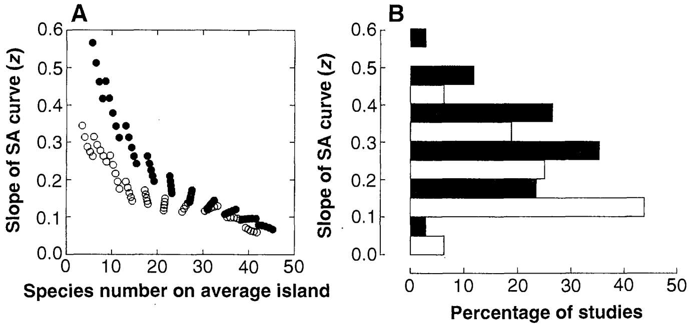

Fig. 2. (**A**) Plot of the slope of the SA curve against the species number on an average-sized island ($m_A = 3$) in the mainland-island (●) and metapopulation models (○), respectively. These results were obtained for the following parameter values: $R = 50$, $Q = 50$, $m_A = 3$, $\sigma_A = 1$, $\sigma_w = 1.5, 1.6, \ldots, 2.0$, and $\log c = -5, -4, \ldots, 5$ in the mainland-island model and $\log c = -15, -14, \ldots, -5$ in the metapopulation model. (**B**) Distribution of empirical *z* values, shown separately for data sets from archipelagoes [mainland-island situations (■), $n = 35$] and mainlands [classical metapopulations (□), $n = 16$]. The difference between the two is significant at the 5% level. Data are from (*30*), omitting data sets in which areas covered less than three orders of magnitude and which hence can be expected to yield unreliable slope estimates.

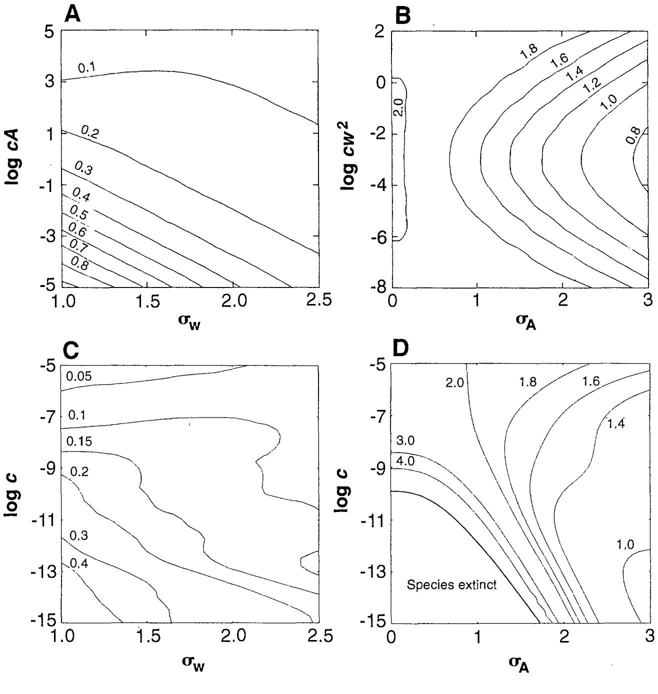

Fig. 3. Dependence of the model-predicted slopes of the SA and DA curves on parameter values. The contour lines join equal *z* values. (**A**) The slope of the SA curve in the mainland-island model as a function of *cA* and σ_w (*19*). (**B**) The slope of the DA curve in the mainland-island model as a function of cw^2 and σ_A for $m_A = 3$ (*19*). (**C**) The slope of the SA curve in the metapopulation model as a function of *c* and σ_w, based on numerical evaluation of the derivative at $m_A = 3$ (*15*). The range of *c* values was selected to roughly match the values used in the respective mainland-island model. (**D**) The slope of the DA curve in the metapopulation model as a function of *c* and σ_A for $w = 1$, based on numerical evaluation of the derivative at $m_A = 3$ (*15*). In the region marked "Species extinct" the value of log *w* is to the left of the vertical asymptote in Fig. 1H (*22*), and the metapopulation goes extinct.

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10. We use the term "island" to refer both to true and

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15. The equilibrium probability of species i occupying island j, p_{ij}^*, which is called the incidence, J_{ij}, is obtained from Eq. 1 as

$$p_{ij}^* = J_{ij} = \frac{C_i^* w_i A_j}{C_i^* w_i A_j + 1} \tag{2}$$

where C_i^* is the equilibrium value of $C_i(t)$. In the mainland-island model, where $C_i(t) = cw_i$, we obtain

$$J_{ij} = \frac{cA_j w_i^2}{cA_j w_i^2 + 1} \tag{3}$$

In the metapopulation model, the incidences can be calculated only numerically. Substituting Eq. 2 into the expression $C_i^* = cw_i \Sigma J_{ij} A_j$, which gives the equilibrium value of $C_i(t)$ in the metapopulation model, we obtain

$$1 = cw_i^2 \sum_{j=1}^{R} \frac{A_j^2}{C_i^* w_i A_j + 1} \tag{4}$$

from which C_i^* can be solved provided that $cw_i^2 \Sigma A_j^2 > 1$, which is a necessary and sufficient condition for species i to persist in the network of islands. The incidences can then be calculated from Eq. 2.

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18. The nonlinear logistic model can be linearized with the logit-transformation, $\log [P/(1 - P)] = a + b \log w$, which we apply throughout this report.
19. Assuming that Q (species number in the pool) is large and that $\log w$ is uniformly distributed with zero mean, we obtain after some calculation the expected number of species on island j as

$$S_j = \Sigma_i J_{ij} = \frac{Q}{4\sigma_w \sqrt{3}} \log \Gamma \tag{5}$$

where (dropping the subscript j)

$$\Gamma = \frac{1 + cA\, e^{2\sigma_w \sqrt{3}}}{1 + cA\, e^{-2\sigma_w \sqrt{3}}}$$

The slope of the SA curve is then given by

$$\frac{\partial \log S}{\partial \log A} = \frac{1 - \Gamma^{-1}}{\Gamma \log \Gamma} \tag{6}$$

The distribution of species i is given by

$$P_i = \frac{1}{R} \Sigma_j J_{ij} = 1 - \frac{1}{2\sigma_A \sqrt{3}} \log \frac{cw_i^2 + q_1}{cw_i^2 + q_2} \tag{7}$$

and the slope of the DA curve is (dropping the subscripts)

$$\frac{\partial \log (P/[1 - P])}{\partial \log w} = \frac{2\, cw^2 q}{(cw^2 + q_1)(cw^2 + q_2)P(1 - P)} \tag{8}$$

where

$$q_1 = e^{-m_A + \sigma_A \sqrt{3}},\ q_2 = e^{-m_A - \sigma_A \sqrt{3}},$$

$$\text{and } q = \frac{1}{2\sigma_A \sqrt{3}} [q_1 - q_2]$$

20. σ_w can be estimated as the standard deviation of the species abundance distribution on the mainland. In 10 examples of invertebrate and bird communities, empirical values ranged from 0.95 to 2.57 (mean = 1.63, SD = 0.62; details can be obtained from I.H. upon request). G. Sugihara [*Am. Nat.* **116**, 770 (1980)] has reported a wider range of values than reported here, but the data in his study do not always represent "local" communities (for example, birds in North America). Using Eq. 3, one can express the parameter combination cA as $cA = w^{-2}J/(1 - J)$, which suggests that, in principle, c can be estimated with data on island areas, species' abundances on mainland, and on their incidences on islands. To aid intuition about the cA values, consider an average species with $w_i = 1$. For such a species, $cA = J/(1 - J)$, and hence the range of cA values in Fig. 3A from 10^{-2} to 10^{2} corresponds to the incidence on average-sized islands ranging from 0.01 to 0.99, which covers a very large range.
21. Denoting the per-year colonization and extinction probabilities by λ and μ, we obtain

$$cA = \frac{\lambda}{\mu} E[w^2]$$

where E denotes the expected value. That the slope of the SA curve depends on the ratio of colonization to extinction probabilities has been suggested by R. E. Ricklefs and G. W. Cox [*Am. Nat.* **106**, 195 (1972)] and M. P. Johnson and D. S. Simberloff [*J. Biogeogr.* **1**, 149 (1974)].

22. The vertical asymptote in Fig. 1H is given by

$$\log w = -\frac{1}{2}\left(\log c + \log \sum_{j=1}^{R} A_j^2\right)$$

The other asymptote has a slope of 2.

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Reduced Ubiquitin-Dependent Degradation of c-Jun After Phosphorylation by MAP Kinases

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The proto-oncogene–encoded transcription factor c-Jun activates genes in response to a number of inducers that act through mitogen-activated protein kinase (MAPK) signal transduction pathways. The activation of c-Jun after phosphorylation by MAPK is accompanied by a reduction in c-Jun ubiquitination and consequent stabilization of the protein. These results illustrate the relevance of regulated protein degradation in the signal-dependent control of gene expression.

The ubiquitin-dependent protein degradation system is used in the cell not just to eliminate proteins that are either damaged or no longer needed. Instead, it fulfills important functions in cell regulation and signal transduction such as the cell cycle–specific degradation of cyclins and the cytokine-induced breakdown of the transcription factor inhibitor IkB (*1*–*5*).

The transcription factor c-Jun is an in vivo substrate for multi-ubiquitination (*6*). We investigated whether the ubiquitin-dependent breakdown of c-Jun is a constitutive process or is regulated and whether it might contribute to signal transduction through c-Jun.

One mechanism by which intracellular information is transduced to c-Jun is the phosphorylation of the protein by MAPK-type enzymes, such as the JNKs and the ERKs

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