Invasion resistance arises in strongly interacting species-rich model competition communities

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ABSTRACT   I assemble stable multispecies Lotka–Volterra competition communities that differ in resident species number and average strength (and variance) of species interactions. These are then invaded with randomly constructed invaders drawn from the same distribution as the residents. The invasion success rate and the fate of the residents are determined as a function of community- and species-level properties. I show that the probability of colonization success for an invader decreases with community size and the average strength of competition (α). Communities composed of many strongly interacting species limit the invasion possibilities of most similar species. These communities, even for a superior invading competitor, set up a sort of "activation barrier" that repels invaders when they invade at low numbers. This "priority effect" for residents is not assumed a priori in my description for the individual population dynamics of these species; rather it emerges because species-rich and strongly interacting species sets have alternative stable states that tend to disfavor species at low densities. These models point to community-level rather than invader-level properties as the strongest determinant of differences in invasion success. The probability of extinction for a resident species increases with community size, and the probability of successful colonization by the invader decreases. Thus an equilibrium community size results wherein the probability of a resident species' extinction just balances the probability of an invader's addition. Given the distribution of α it is now possible to predict the equilibrium species number. The results provide a logical framework for an island-biogeographic theory in which species turnover is low even in the face of persistent invasions and for the protection of fragile native species from invading exotics.

Elton (1) suggested that species-rich communities are more resistant to invasion by exotics than are species-poor communities. Later Elton's hypothesis became embroiled in debates over the association, if any, between community stability and diversity (2). Theoretical explorations of this connection showed that, if anything, diverse systems are more likely to be unstable (3). Yet, stability analyses for these models are performed by looking at the community's asymptotic response to small perturbations away from equilibrium. Invasion resistance, on the other hand, deals with an entirely different concept: the dynamics of the community in a new state-space involving the added species; there is no simple connection between this and the asymptotic stability of the community prior to invasion. There is growing evidence for Hawaiian birds and Pacific lizards that later introduced species have caused problems for previous introductions (4–6). Additional empirical support for a connection between invasion-resistance and community size and complexity comes from Drake (7) and Robinson and Dickerson (8) working with experimental microcosms containing bacteria, plankton, and plankton feeders.

Here I show that the probability of colonization success for an invader decreases with community size and structure. I show that communities composed of many strongly interacting species limit the invasion possibilities of most similar species. These communities, even for a superior invading competitor, set up a sort of "activation barrier" that repels the competitors when they invade at low numbers. This "priority effect" for residents is not assumed a priori in my description for the individual population dynamics of these species; rather it emerges because species-rich and strongly interacting species sets have alternative stable states that tend to disfavor species at low densities. In nature, invasion success will be determined, in part, by the particular biological attributes of the invaders (their adaptation to the physical environment, their life history, etc.) and in part by the community-level attributes of the places that they invade. These models point to community-level rather than invader properties as the strongest determinant of differences in invader success rates.

MODELING METHODS

My immediate motivation is to assemble stable communities that differ in resident species number and average strength (and variance) of species interactions and then to invade these communities with randomly constructed invaders drawn from the same distribution as residents. I then determine invasion success and the fate of the residents, as a function of community- and species-level properties. Here, I deal only with species on a single trophic level modeled by the familiar Lotka–Volterra competition equations.

Construction of the Resident Community. The resident community is constructed in two alternative ways:

(i) Random α values chosen from a uniform distribution. A community matrix A is produced with terms α_{ij} describing the species interactions. The interspecific, off-diagonal, terms of the interaction matrix A are simply drawn from a uniform (rectangular) distribution from 0 to some upper limit (max) and the intraspecific terms are set to 1. This method lacks ecological realism but allows for great flexibility in choosing the statistical properties of the elements of A. It has a long history in the ecological literature (3, 9, 10).

The mean α_{ij}, the variance of α_{ij}, and the covariance between α_{ij} and α_{ji} will not change with community size. But, since stability is not guaranteed, and since only stable core communities are selected for invasion, there will be a weeding-out of the unstable communities. This selection may bias some statistical properties of the As that are actually used for invasion trials compared to those discarded. I have quantified this bias and found it to be unimportant in accounting for the major trends (11).

(ii) Resource utilization overlap matrices. First a resource utilization matrix (U) is constructed with dimension n consumer species by M resources. The elements u_{ji} of U give the rate of utilization of resident consumer j on resource i. There are a number of possible ways to assign these u values. The simplest is to draw them randomly from a uniform distribu-

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tion [0, 1] or [0, 1.6]. However, observed resource utilizations from many vertebrates (e.g., from stomach contents) usually have a distribution of prey items that more closely approximates a log-normal or broken-stick distribution than a uniform distribution. Hence, for realism, I assign utilization rates by a broken-stick distribution (see ref. 12 for details).

The U matrix is converted into a community matrix A with terms α_{ij} describing the species interactions based on the degree of interspecific resource overlap, using standard niche formulas (12). The resulting α values have a skewed bell-shaped distribution from 0 to slightly more than 1; the mean is about 0.45.

Significantly, when A is constructed in this manner it is guaranteed to be positive definite [all its eigenvalues are positive (13, 14)]; moreover, the resulting community will be globally stable if feasible (14).

Population Dynamics and Stability Determination. The population growth of species i constructed by either of the methods above is assumed to follow the Lotka–Volterra competition equation:

$$\frac{dN_i}{dt} = \frac{r_i N_i}{K_i} \left(K_i - \sum_{j \neq i}^{n} \alpha_{ij} N_j \right). \qquad [1]$$

All species have intrinsic growth rates (the r values) set to 0.5 and the carrying capacities (the K values) chosen in a way to guarantee that the community is "feasible"—i.e., that the equilibrium densities of all n consumers are greater than 0. The all-positive nature of A guarantees that there will exist an n-dimensional set of such K vectors that yield feasibility (15). By adding the constraint that the sum of all the K values must equal some constant (e.g., n), one can use linear programming to solve for the region of K-space (i.e., the range of K values for each species) that satisfies feasibility and that intersects the constraint surface $\Sigma K_i = n$. [Vandermeer (16) presents the method for two species.] I select the midpoint of that feasible K-space as the K-vector. The positive-definite nature of A, constructed as overlap matrices, produces a starting (= core or "target") community of any arbitrary size that is both feasible and stable. On the other hand, core communities assembled by randomly chosen α values are not necessarily stable if feasible, so after constructing the K-vector, I test the stability of the feasible equilibrium point. Unstable communities are discarded and only stable–feasible communities are saved for subsequent invasion. Community stability for an n-species community is determined by seeing if the community returns to its n-species equilibrium point after small perturbations away from it.

Invasions. For random α matrices, the invader's interaction terms with all the residents are drawn from the same distribution as that of the residents' interactions with themselves. Overlap-constructed resident communities are invaded by adding a new row to the resource utilization matrix U, giving an augmented matrix U' with dimension ($n + 1$ consumers by the same M resources). The new community matrix A' (which is $n + 1$ by $n + 1$) is created by using Eq. 1 and the augmented U' instead of U. Note that the n by n top-left compartment of A' will be identical to A. The K of the invader (K_i) is chosen as the average of the residents, which is constrained to always be 1.0 regardless of species number. Thus the invader's K, and its α_{ij} and α_{ji}, terms, come from the same distribution as that used to construct those of the residents. Increasing the K of the invader so that it is greater (or less) than that of the average resident simply has the effect of increasing (or decreasing) its invasion success and increasing (or decreasing) resident replacement rates. The flavor of all the results below is not otherwise altered. I also performed a smaller duplicate set of runs with the r of the invader twice

that of the resident ($r_i = 1.0$). There were no significant differences in outcome (11).

The invasion process is simulated by introducing the invader at low numbers ($K_i/1000$) into a core community of resident species at their community equilibrium densities. The resulting species' dynamics are followed over time by numerically integrating the Lotka–Volterra differential equations describing each species population growth using the Euler method. The community trajectory is followed until it settles into a new equilibrium defined by per-iteration community change reduced below a threshold value (less than 0.000001% movement in Euclidean space from the previous state). At the new equilibrium, the number of species, the presence or absence of the invader, and the number of extinct residents are determined. Each core community is invaded 10 times and between 30 and 80 different core communities are chosen for each combination of parameters.

RESULTS

An invasion can result in one of the following four possibilities. (*i*) *Community augmentation.* The invasion is successful and the community absorbs the invader, growing in size by one species. (*ii*) *Rejection failure.* The invader is repelled and the resident community remains intact. (*iii*) *Indirect failure.* The invader population initially grows and in the process causes other species' abundances to change; these changes, in turn, create a situation which is less favorable for the invader, and it begins to decline ultimately to extinction. In the process the resident community is "fractured" so that some residents become extinct. (*iv*) *Replacement.* The invader succeeds at the expense of one or more residents. Indirect failure presents an interesting and somewhat counterintuitive theoretical possibility. An invader, even at low numbers, can upset a community's stability, cause resident extinctions, then disappear without a trace. This occurs infrequently compared to rejection failure in these simulations. Below the two failure rates are summed to produce a total invader failure rate.

Invasion Outcome as a Function of Community Size. Fig. 1 shows the frequency of these three alternative outcomes as a function of core community size. Core communities are constructed as random α values and two of the panels are for different values for the range of interaction strengths (Fig. 1A: α values from 0 to 1; Fig. 1B: α values from 0 to 1.6). Augmentation frequency declines sharply with species number and appears to asymptotically approach 0. Both failure frequency and replacement frequency increase asymptotically. Fig. 1C shows similar results for communities constructed as overlap matrices.

Invasion Outcome as a Function of the Strength of Interspecific Interactions. Comparing Fig. 1 A and B, it is apparent that failure rates are much higher, and success and replacement rates much lower, for communities with strong interspecific interactions (Fig. 1B) compared with weaker ones (Fig. 1A). This effect is explored in more detail in Fig. 2, where I plot the three invasion outcomes as a function of mean interaction strength for core communities of four species. As interaction strengths become large, residents become protected from competitive replacement by invaders.

Resident Extinctions. As core community size increases the frequency of replacement grows and during an individual replacement event, more than one resident may become extinct. The mean number of residents becoming extinct per invasion event (Fig. 3; the extinction curve) and per replacement event (11) increases supralinearly with both community size and α.

Existence of an Equilibrium Species Number. Imagine that communities are continually being pelted by invaders. Scale

A. α uniform [0, 1]

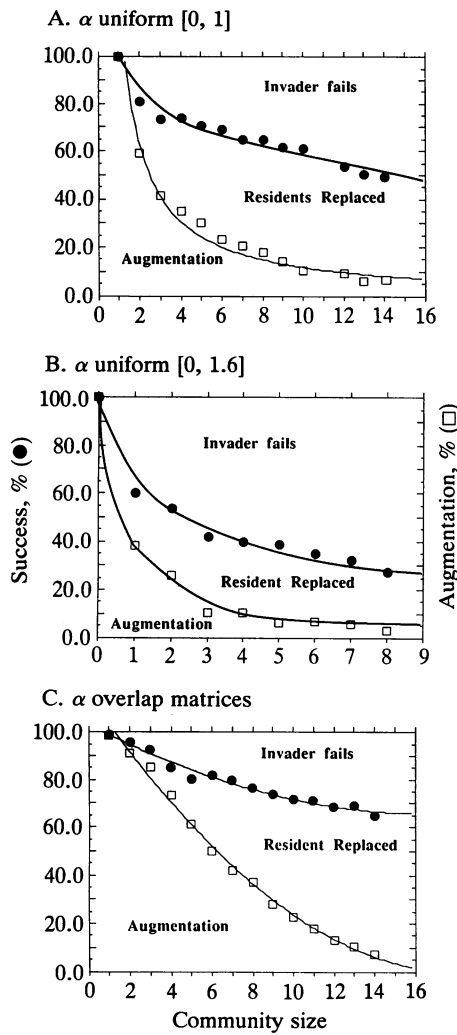B. α uniform [0, 1.6]

C. α overlap matrices

FIG. 1. Frequency of invader success, augmentation, and replacement events as a function of the size (number of species) of the core community being invaded. Note that percent success is the sum of augmentation and replacement. (*A*) Species interaction terms (α values) are drawn from a uniform distribution [0, 1.0]. (*B*) α values are drawn from a uniform distribution [0, 1.6]. (*C*) α values are constructed as resource overlaps.

time according to the average interval between invasions. With these mental constructs we can visualize the dynamics of faunal buildup. Since the probability of extinction for a resident species increases with community size and the probability of successful colonization by the invader decreases, an equilibrium community size will result wherein
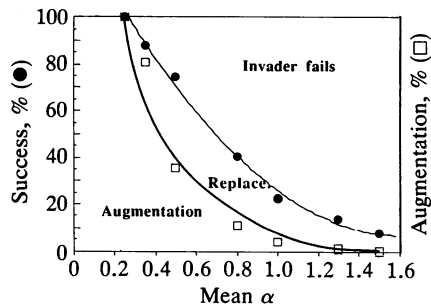

FIG. 2. Various invasion outcomes (as in Fig. 1) plotted as a function of the mean α (all α values drawn from uniform distributions from 0 to twice the mean); all results are based on invasions of 4-species core communities.
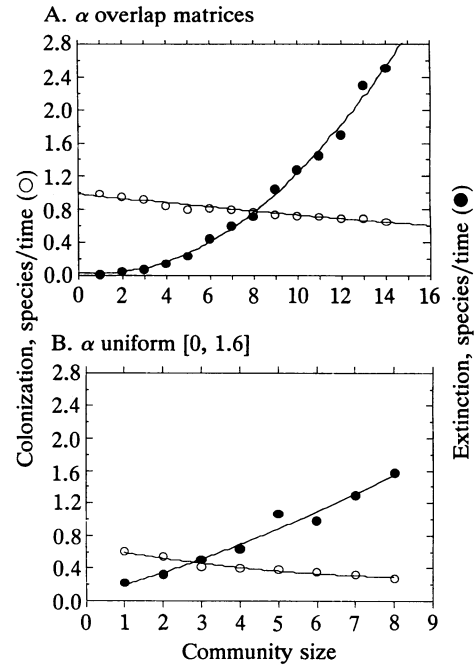
A. α overlap matrices

B. α uniform [0, 1.6]

FIG. 3. Extinction rate per invasion attempt (species/time) and colonization rate per invasion attempt (species/time) plotted as a function of core community size. Where the curves intersect, community size will be maintained at equilibrium. The curves are the best least-squares fit to a quadratic. (*A*) α values are overlap matrices. (*B*) Random α values from [0, 1.6].

the probability of a resident species' extinction just balances the probability of an invader's addition. This is illustrated in Fig. 3; extinction rates are calculated as the average number of residents becoming extinct per invasion attempt (i.e., per time interval). The equilibrium number of species is about 8 when A is constructed as an overlap matrix, about 5 when the α values are drawn from a uniform distribution on [0, 1.0] (not shown), and falls to about 3 when α is drawn from [0, 1.6].

The similarities between this equilibrium species number (*S*) and that of the equilibrium theory of island biogeography (17) are superficial; the processes are complementary rather than overlapping. An equilibrium *S* arises in equilibrium island theory because of an assumption that the colonization rate must decline with *S* because the mainland species pool is finite; here the species pool is infinite. In the equilibrium theory the extinction rate rises with *S* because each species is assumed, *a priori*, to have some finite probability of extinction—the more species, the more likely that one or more will go extinct in a given time interval. On the other hand, here I assume that per-species extinction probabilities are 0 in the absence of invasion; the extinctions that occur result exclusively from invasions (also see *Discussion*).

Given the distribution of α, it is now possible to predict the equilibrium species number. As the average (and with it, the variance) in interspecific interaction strength increases, the equilibrium species number reached by the invasion–extinction process decreases. Associated with this decline is a sharp decline in the species turnover rate at equilibrium from about 0.9 species/time for mean α = 0.3 to only 0.09 species/time for mean α = 1.3. (Recall that the time interval is scaled to one invasion interval.)

Invasion Success: Relative Role of Between-Community vs. Between-Invader Differences. Some theoretical insight into this question can be gained by modifying the invasion protocol so that a single core community is invaded sequentially by 20 randomly chosen invaders instead of 10 as before (this provides a better sample for per-community statistics). This is repeated three separate times for the same core commu-

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nity, and for each of the three replicates, statistics for success rates based on the 20 invasion trials are calculated. Then another random core community is constructed and it is invaded in three replicates of 20 trials each. This is repeated for a total of 10 core communities and an analysis of variance is performed to compare the magnitude of between-community differences relative to between-invader (but within-community differences) in success and augmentation frequencies.

I have performed this analysis for core communities of size 3, 7, and 10 species. α values were chosen from a uniform distribution between 0 and 1. For all sizes of core communities, the between-community variance in invader success rates is between 6 and 7 times greater than the between-invader differences as reflected by the F ratios. All F values are highly significant ($P < 0.0004$). Since the invader's K was always the same (set equal to that of the average resident), perhaps it is not too surprising that variance in invasion success is due more to differences among communities being invaded than differences among invaders. In a separate simulation I repeated the above analysis for 7-species core communities but I chose the K for each invader at random from the K values of the 7 residents (with uniform probability). Thus the invaders had the same variance in K as the residents themselves. As expected the F ratios are less but the between-community variance in invader success rates is still over 5 times greater than the between-invader differences as reflected by the F ratio (11)!

DISCUSSION

Why Do Species-Rich Communities Repel Invaders? As amply demonstrated by previous work (e.g., ref. 3), large randomly constructed communities are more likely to be unstable than small ones. As the community enlarges, some species are more likely to shake loose. This is the main reason for the decline in augmentation rates with community size (and interaction strength). As augmentation declines, invader success rate must decline with it. This is not, however, the complete story. By plotting the ratio of replacement frequency (R) to failure frequency (F), we get an inverse index of invader success that is independent of the frequency of augmentation (Fig. 4) and is a measure of the resident community's resilience to invasions. During both replacement and failure events at least one species becomes extinct; the R/F ratio measures whether that extinction is more frequent for residents than for invaders. If extinction is equally likely for both sets of species then R/F is 1.
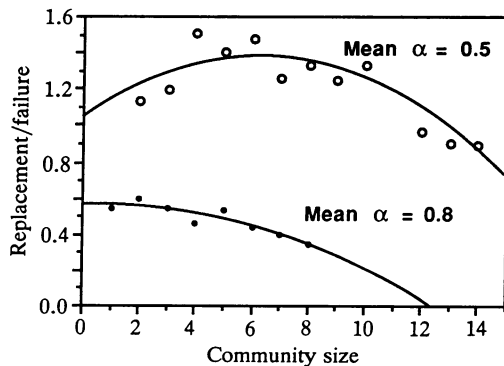

FIG. 4. Ratio of replacement frequency to invader failure frequency as a function of the species number in the core community being invaded. Species interaction terms α are drawn from uniform distributions [0, 1.0] and [0, 1.6]. The curves are the best least-squares fit to quadratics.

We can form a null expection about how the relationship between R/F and species number (S) should look by considering what might happen if all that is going on in these competitive systems can be reduced to simply the outcome of pairwise interactions. There are three possible outcomes to pairwise coexistence, and we can denote the probabilities of each for the case of a single resident species as invader outs the resident (w), invader loses to resident (f), and invader coexists with resident (c). The sum $w + f + c = 1$. The more species there are, the more likely there will be some resident that in isolation would exclude a given invader. Making this argument concrete, an invader failure means that it would never win or coexist with any of the S residents in isolation. If indeed these contests were independent events failure would equal $1 - (w + c)^S$ and thus failure rates would increase with S but at a diminishing rate (as it does). A replacement event means that in pairwise contests an invader would win one or more times out of S trials or, put another way, the invader would never lose or coexist in S trials. If indeed contests were independent, the probability of replacement $R = 1 - (f + c)^S$. This would suggest that replacement rates increase with S at an ever-diminishing rate, which is roughly what is observed. Form the ratio

$$\frac{R}{F} = \frac{1 - (f + c)^S}{1 - (w + c)^S}. \qquad [2]$$

If $f = w$ this ratio equals 1, regardless of S. If $f > w$ R/F increases monotonically with S, but if $f < w$ this ratio decreases with S. In any event, R/F is monotonic.

As Fig. 4 shows, the relationship between R/F and community size is more complex. It is roughly parabolic when α values are drawn from a uniform distribution. First, consider the top curve in Fig. 4 for mean $\alpha = 0.5$. When the core community size is simply one species, all invasions are successful and lead to community augmentation ($f = w = 0$), hence no replacements or failures occur (this is because the K values are equal in this case, at 1.0, and no α is greater than 1.0: two-species coexistence is inevitable). At a community size of 2 R/F is close to 1.0, but as species number increases, although replacement and failure rates both increase, the former increases faster than the latter and the R/F ratio rises.

As community size increases still more a new trend emerges: the R/F ratio now begins to decline and eventually drops substantially below 1.0. A clue to what is happening in this region is provided by the lower curve for mean $\alpha = 0.8$ (Fig. 4). Here the entire curve for R/F is at or below 1.0. All these communities are resistant to the invader and the relative success of the invader (R/F) consistently declines with species number. This occurs in spite of the fact that for these paratmeters, $f > w$ in two-species competition, leading one to expect R/F to decline with S as outlined above. The ability of these communities to repel invaders is produced by the emergence of multiple domains of attraction in large and/or strongly connected communities (10).

To see how this happens, consider the textbook example of a two-species Lotka–Volterra competition system with an interior equilibrium point that is unstable. Further imagine that both species have the same K and r and $\alpha_{12} = \alpha_{21} > 1.0$. There are two stable end points: either species 1 wins and reaches its carrying capacity K_1 or species 2 wins and the system reaches K_2. The outcome depends on which species is initially the most abundant. If we begin with species 1 at its equilibrium density of K_1 and introduce a few individuals of species 2, the invasion will be unsuccessful. Similarly for the same two species, if we reverse resident and invader, species 2 alone will repel the invasion of species 1. Both species are equally competitive and could competitively exclude the other; the outcome is decided by who gets there first. The

existence of multiple domains always gives the *dis*advantage to species which, although perhaps equally competitive with the others, are late-comers and at low frequency. In this way a priority effect is produced for established residents, giving them a competitive edge over invaders. The invader can enter only if it is introduced in very large numbers.

Gilpin and Case (10) found that the frequency of multiple domains in Lotka–Volterra competition systems increases exponentially with community size and with average interaction strength. The $(n+1)$ species equilibrium point is not a globally attracting node; infact, the fraction of state space over which it attracts decreases with species number (10) and communities with many species, even if all α values are less than 1, may have many domains of attraction. A corollary of this effect is that invader extinction rate (relative to that of residents) will increase with community size and interaction strength, producing the patterns in Fig.4. Overlap-type A matrices do not exhibit this phenomenon (11). Such matrices can have only one domain of attraction regardless of size (14) and, as expected, they show no trend for R/F to decrease with community size in my simulations (11).

Invasion and Indirect Interactions. It is now well appreciated in the ecological literature that when more than two species compete, the net effect of one competitor on another may be beneficial within the context of the entire community network (18–20). This advantaging arises because a species' enemy's enemy is often its ally. Not simply an oddity, such indirect mutualisms may be quite common (refs. 21 and 22; A. L. Stone and A. Roberts, personal communication). Less well appreciated is the fact that an inferior competitor may thus be protected from competitive exclusion by an invading superior competitor within the context of the resident community to which it belongs.

To determine the role of indirect effects in protecting residents, I modified the invasion scheme to construct two focal species: species 1 and an invader, both with identical $K (= 1.0)$ and with $\alpha_{i1} = 1.4$ and $\alpha_{1i} = 0.6$. In isolation, regardless of initial densities, the invader (i) will always competitively replace species 1. To imbed resident species 1 in a community of other competitors, I choose K values as before except that I fix $K_1 = 1$. Consquently, some of these randomly generated core communities are unfeasible and I throw these out, keeping only the remainder for further invasion trials. As before the invader has a $K = 1.0$ (still the mean of all the resident species' K values), and its α terms with all of the residents except species 1 are chosen at random from [0, 1.2]. This means that the depressive effect of the invader on species 1 exceeds any other interaction in the community.

When the core community is only species 1, it is competitively replaced by the invader every time; yet, with the addition of only a single additional resident species, the invader's success falls off to 82% while 76% of the time the invader competitively excludes species 1. By the time the core community contains seven species, invasion success has dropped to about 53% and only 38% of the time is the inferior species 1 competitively excluded by the invader.

Often in conservation management one wishes to protect a species known to be competitively inferior to a spreading exotic. These simulations provide theoretical justification for the prevailing wisdom that undisturbed species-rich communities may often be better able to accomplish this goal (1, 23).

Implications for Island Biogeographic Theories. MacArthur and Wilson's (17) ground-breaking treatment of the equilibrium theory of island biogeography dealt with interspecific interactions only implicitly by sweeping them into a verbal explanation for the expected concavity of the extinction rate versus species number curve. Yet detailed studies of the distribution of island species often show patterns in species assortment that are most plausibly explained by interspecific interactions (24–28). Lack (29) suggested an alternative to the equilibrium theory of island biogeography. He believed that island isolation was not an important factor limiting colonization success and that island area chiefly affected species number through its effect on habitat diversity. He went on to propose that species turnover was limited or nonexistent on these islands. Although islands might be continually tested by invaders, these invasions were thought not able to take hold because the residents already made use of all the available resources and habitats. In this theory an island's species are uniquely adapted to their biotic environment and this gives them an ecological advantage over invaders, even those arising from places with similar physical environments. The results presented here provide a logical framework for an island-biogeographic theory based on species interactions and invasions without invoking *ad hoc* coevolution, inherent superior adaptation of residents relative to invaders, or *a priori* resident priority effects. This theory, however, diverges from Lack's in that he imagined that habitat expansion and adaptation to island habitats by residents were responsible for making communities resistant to invasion rather than multiple stable points emerging in systems with much diffuse competition, as in my model. In an important recent study, Schoener and Adler (25) analyzed the island distribution patterns of selected sets of bird and lizard species in the Bahamas. Their work suggests a role for diffuse competition not unlike that envisioned here. After controlling for differential habitat affinities of the species, they found frequent negative three-species interactions, often in the face of significant negative (or even positive!) pairwise interactions.

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