

A Neglected Facet of Island Biogeography: The Role of Internal Spatial Dynamics in Area Effects

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The classical theory of island biogeography has as its basic variable the presence or absence of species on entire islands, and as its basic processes colonization and extinction rates on entire islands as functions of island area, distance, and so forth. Yet for many organisms with limited dispersal abilities, it may be more reasonable to consider larger islands as comprised of an ensemble of local populations coupled by within-island dispersal. Conceptual arguments and a simple patch occupancy model are used to examine the potential relevance of such internal spatial dynamics in explaining area effects, expressed via the probability that a species is present per unit area as a function of total island area. The model suggests that strong area effects depend on a rather fine balance between local colonization and extinction rates. A fruitful direction of future research should be the application of patch dynamic theory to classic island biogeographic questions and systems. © 1992

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Surely the most thoroughly supported empirical generalization of community ecology is the species–area relationship—the observation that, in general, larger areas contain more species than do smaller areas. Explaining the observed relationship between island area and species diversity was a principal motivation behind the development of the equilibrium theory of island biogeography (MacArthur and Wilson, 1967). Elucidating the underlying causes of the species–area relationship has been the focus of much and continuing controversy (Williamson, 1989), ranging from the proper statistical description of the relationship (Connor and McCoy, 1979), to the relative importance of colonization–extinction dynamics (Diamond, 1985), purely sampling phenomena (Coleman, 1981), and the association of increased habitat heterogeneity with increasing island area (McGuinness, 1984) as explanations for the phenomenon. In this paper, I present conceptual arguments and a simple model suggesting that a fruitful way to think about area effects in island biogeography may be to view large islands as comprised of “metapopulations” of juxtaposed smaller

patches. A full understanding of the species-area relation in island biogeography requires an analysis of the internal spatial dynamics of islands.

The empirical literature on the species-area relationship, at least for data from islands (rather than sampling or "collector" curves in continental regions), contains several distinct kinds of species-area curves (Holt in press). By far the more common in the literature is what I call the *total species-area curve*, in which for each of a set of islands varying in size, one counts the total numbers of species present, and then regresses this number against island area. One of the difficulties that has faced workers trying to untangle the causes for observed species-area effects is that large islands may simultaneously have larger sample sizes, lower rates of extinction, higher rates of colonization, and overall more spatial heterogeneity, than do small islands. That this conundrum arises is not really all that surprising, given that the basic unit of analysis in total species-area curves—entire islands—is by definition a non-uniform sampling unit.

Indeed, it may be misleading to compare the total species lists among islands differing in size, at least if one hopes to interpret the species-area relationship in terms of underlying population and community mechanisms that operate on spatial scales much smaller than entire islands. A fairer comparison is to take community censuses in defined sampling areas of fixed size and shape, across islands varying in area. When one regresses this estimate of local, within-sample species richness against total area, one generates another kind of species-area curve, which I call the *standardized species-area curve*.

Compared to the numerous total species-area curves to be found in the literature of biogeography and ecology, standardized species-area curves are rather rarely reported. Kelly *et al.* (1989) have recently argued that the construction and analysis of standardized species-area curves is essential if one is to discriminate among alternative hypotheses for an observed total species-area relationship. For a given set of islands, the total species-area curve and the standardized species-area curve will be the same only in the very special circumstance of having all species on an island found in all sampling units. This will usually not be the case. Indeed, for some taxonomic groups there appears to be at best a weak or equivocal relation between sample species richness and island area, despite strong relationships between total species richness and area. For examples, Westman (1983) found that for xeric shrubs censused in standardized samples on the California Channel Islands, the number of species was independent of island area. A similar example from my own work on successional dynamics in fragmented habitats is shown in Fig. 1 (Holt and Robinson, manuscript). The data show that there is no effect whatsoever of fragment size on the number of species found in permanent sample quadrats, despite

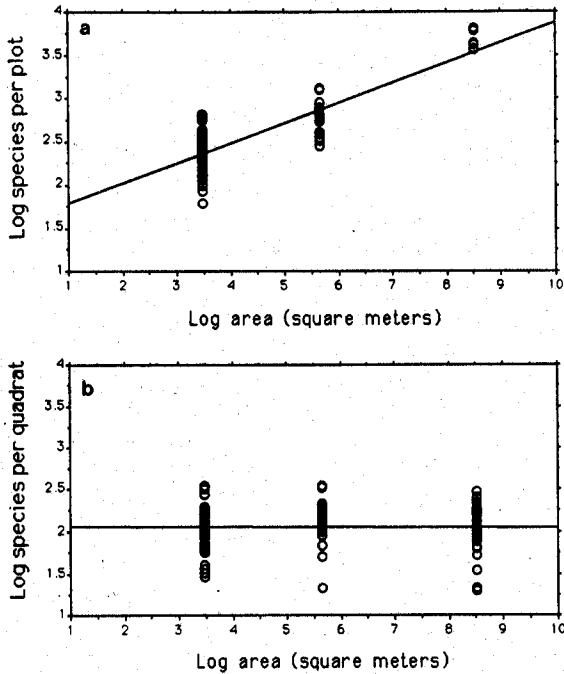


FIG. 1. Species-area relations for vascular plant species in an experimental study of the effect of habitat fragmentation on succession at the Nelson Environmental Study Area, Kansas. The system consists of an archipelago of 106 patches, separated by a low turf (maintained by intense mowing) that provides a dispersal barrier; the patches are clearly island-like in important respects. The data shown are complete censuses within patches. (a) Total species-area relation, and complete censuses within permanent m^2 quadrats placed in each patch; (b) Standardized species-area relation. The straight lines are fitted regressions. Large patches have more total species than small patches, but no more species per unit area. The methods and data set are described fully in Holt and Robinson (manuscript).

a strong total species-area relationship. Kelly *et al.* (1989) sampled vascular plant species in fixed quadrats on a set of islands in Lake Manapouri, New Zealand, as well as surveying the entire flora. The percentage of variation in species richness explained by island area was reduced from a highly significant 92% to a statistically insignificant 17% and 10% for two distinct vegetation types. All of these examples involve vascular plants. By contrast, in West Indian birds, both local species richness and total species richness increase with island size (Ricklefs, 1987). The relationship is considerably stronger in the latter case. Nonetheless, in these bird communities, local species richness reflects the area of the island in which the local community is embedded. Likewise, Wilson (1961) in his classic paper on Melanesian ants compared ant communities in areas

within New Guinea and on equal-sized offshore islands and demonstrated a very marked reduction in local species richness on the islands.

The theme I explore in this paper is that such differences in standardized species-area curves may reflect differences in the spatial dynamics of colonizing species within islands. The model presented below suggests that West Indian birds and Melanesian ants may show a standardized species-area curve with positive slope, whereas vascular plants in some communities do not, in part because many species of birds and ants may be more mobile within islands than are many plant species.

The dynamical theory of island biogeography developed by MacArthur and Wilson (1967) has as its basic variable the presence or absence of a species on an entire island taken *in toto*. Predictions about the species-area relationship follow from assumptions about the relation between rates of extinction or colonization and island size. Yet colonization usually does not take place across an entire island in a flash. Instead, propagules land at one or a few sites, which then provide nuclei for the expansion of the colonizing species through the rest of the island. In like manner, the last stages of extinction often find an island population hanging on in a few remnant sites. I suggest that understanding the spatial structure and dynamics of populations within islands may be important for understanding the strength of area effects, *per se*. In this paper, I present a simple model examining this idea.

Consider a small island which can be colonized by a given species from a distant source pool, and a randomly chosen sample area equal in size and distance from the source pool as the isolate, but embedded within a large island (Fig. 2). For simplicity, let us assume that the abiotic environment and rate of long-distance colonization per unit area are independent of island size (but see Saunders *et al.*, 1991). There are three conceptually distinct processes by which the remainder of the large island can influence the probability that a species will be present in the sample area. The first two both concern enhancements in local colonization rates, but result from distinct historical pathways. The third involves a reduction in local extinction rates.

1. *Stepping Stone Effect.* The remainder of the island may augment the initial rate of colonization of the sample area, because the species may first become established elsewhere on the island and then spread to the sample area by within-island dispersal. This is analogous to the role of stepping stone islands in enhancing colonization on distant oceanic islands (MacArthur and Wilson, 1967; Gilpin, 1980).

2. *Spatial Storage Effect.* If the sample area was the initial site of colonization, surrounding areas can be colonized from this original nucleus. Should the species go extinct on the sample area, there can be

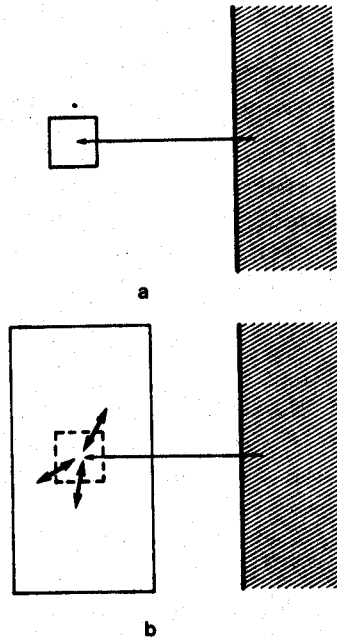


FIG. 2. (a) A small island at a given distance from a source pool for colonizing organisms. (b) A sample area, equal in size and distance to source pool as the small island, placed within a large island. The probability that a species is present in the sample area will be influenced by a combination of long-distance dispersal from the source pool, and within-island dispersal.

rapid re-colonization from surrounding inhabited areas. This "spreading of risk" (den Boer, 1968) is reminiscent of Chesson's storage effect, in which a species may persist despite years of low recruitment because of a long-lived adult age-class (Chesson, 1986). It also in some respects is analogous to the stabilizing effect of dormancy (including delayed germination) in fluctuating environments (e.g., Venable and Brown, 1988).

3. Internal Rescue Effect. If the population in the sample area fluctuates to a low density, at which it would be in danger of extinction on the isolated small island, the presence of other populations nearby at higher densities may allow "spillover" of individuals, buffering fluctuations in the local population and reducing the chance of extinction in the sample area. Brown and Kodric-Brown (1977) observed in an experimental field system that rates of extinction increased with distance from a source pool, and suggested that this was because low-density populations are enhanced by immigration. This effect should often be strong when considering a sample area within a large island.

In a full analysis of these effects for a species found across a range of

island sizes, one would first decompose each island into spatial arrays of juxtaposed cells, and then characterize the dynamics of the subpopulation found in each cell (including of course movement among cells) (e.g., Fahrig and Merriam, 1985). In such a representation, island size corresponds to the number of juxtaposed cells. To generate the total species-area curve from a spatially explicit model, one needs to determine the total probability that a species is present anywhere in a cellular matrix of defined size. To arrive at the standardized species-area curve, one instead aims at determining the probability that a species is present in a randomly chosen cell, as a function of the number of cells comprising an island. At an intermediate level of complexity between a full-blown, spatially explicit population model, on the one hand, and the rather abstract presence/absence of a species on entire islands (as in the classical MacArthur-Wilson model), on the other, one can monitor the presence/absence of a species on each cell within an island, thus bringing to bear on the questions of island biogeography a patch dynamic perspective (Hanski and Gilpin, 1991).

As a step toward this full analysis, here I present what may be the simplest imaginable model that can illustrate the three effects outlined above. I contrast the dynamics of an ensemble of "singlets," isolated cells that can only be colonized (if at all) from some distant source pool, with the dynamics of an ensemble of "doublets," where the latter are comprised of two juxtaposed singlets which can influence each others' respective colonization and extinction rates. Some justification for an analysis of a doublet model comes from the work of Quinn and Hastings (1988) on extinction in populations divided among noninteracting patches; in their model studies, they observed that the interesting qualitative effects of a multipatch model could also be observed (albeit less strikingly) even in two-patch systems. I assume (following Levins and Culver, 1971, and many subsequent authors) that each ensemble is large enough that its dynamics can be reasonably described by differential equations, the variables of which consist of the fraction of the ensemble falling into each of various mutually exclusive states.

As in standard island biogeography, singlets can exist in two states, 0 (species absent), or 1 (species present). Let $p(t)$ be the fraction of isolates that contain the species at time t , e be an instantaneous rate of extinction, and c an instantaneous rate of colonization of empty singlets. The rate of change in patch occupancy is described by

$$dp/dt = c(1 - p(t)) - ep(t), \quad (1)$$

and at equilibrium the fraction of patches occupied is

$$p' = c/(c + e). \quad (2)$$

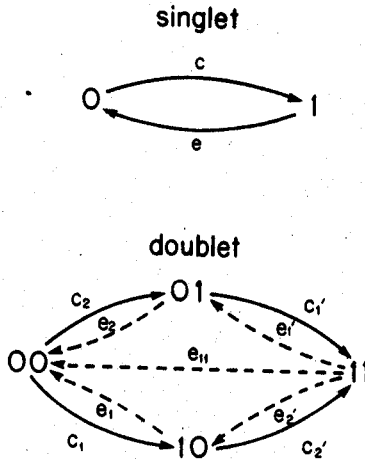


FIG. 3. Transitions between the two states of a singlet—0, 1—and among the four states characterizing a doublet: (00), (10), (01), (11). See text.

In the usual island biogeographic model, one lets c and/or e be functions of island area, distance, etc., and proceeds from there. Here, I instead imagine that a two-fold increase in island area can be represented by linking two singlets into one doublet. A doublet can be described by four states: 00 (species completely absent); 10 (species present in only one of the two halves of the island); 01 (species present in just the other half); 11 (species present everywhere). In our ensemble of doublets, the fraction found in each of these four states are respectively denoted p_{00} , p_{10} , p_{01} , and p_{11} , which of course sum to one. Figure 3 depicts the transitions which can occur among these four states and the rate parameters governing these transitions. This diagram assumes that there are no direct transitions from 00 to 11, which is to say that colonizations are initially localized on one end of the island or the other. By contrast, island-wide catastrophes (e.g., hurricanes, tidal waves) do happen and could lead to island-wide extinctions (11 → 00). For simplicity, I mostly ignore the latter possibility here. This in effect assumes that extinctions occur slowly enough that a species on its last legs is restricted to one half of the island, rather than disappearing simultaneously throughout the island.

We will arbitrarily label one half of the island 1, and the other half, 2. The quantities c_i scale the rate of colonization of half i of the island, given that the other half is empty. The quantities c'_i determine the rate of colonization of island half i , given that the other half is already colonized. In like manner, e_i is the rate of extinction for half i of the island, given that the other half is empty, whereas e'_i is the rate of extinction of that half when the other half continues to sustain the species.

The system of differential equations describing this system corresponding to Eq. (1) for the "singlet" is written out in Table I. At equilibrium, the fraction of doublets found in each state is as shown in Table I. The probability that the population is found on a randomly-chosen half of an island (= the defined sample area) is $p^* = p_{11} + (p_{10} + p_{01})/2$. By comparing this to the equilibrium occupancy predicted by Eq. (2), one can

TABLE I

"Singlet" model

Two possible island states: 0, 1

 p_i = fraction of island in state i

Model

$$\frac{dp_1}{dt} = c(1 - p_1) - ep_1$$

At equilibrium

$$p_1^* = c/(c + e)$$

"Doublet" model

Four possible island states = 00, 10, 01, 11

 p_{ij} = fraction of islands in state ij

General model

$$\frac{dp_{10}}{dt} = c_1(1 - p_{10} - p_{01} - p_{11}) - (e_1 + c'_2)p_{10} + e'_2p_{11}$$

$$\frac{dp_{01}}{dt} = c_2(1 - p_{10} - p_{01} - p_{11}) - (e_2 + c'_1)p_{01} + e'_1p_{11}$$

$$\frac{dp_{11}}{dt} = c'_2p_{10} + c'_1p_{01} - (e'_1 + e'_2 + e_{11})p_{11}$$

$$\begin{aligned} \text{Let } D = & (e_{11}c_1c'_1 - 2e_{11}c_1c_2 - c_1c_2c'_1 + e_{11}c'_1c'_2 + c_1c'_1c'_2 - c_1c_2c'_2 \\ & + c_2c'_1c'_2 + e_{11}e_1c'_1 + c_2e_1c'_1 + 2c_1c_2e'_1 + c_1c'_2e'_1 + e_{11}c_1e_2 \\ & + e_{11}e_2c'_2 + c_1e_2c'_2 + e_{11}e_1e_2 + c_1e_2e'_1 + e_2c'_2e'_1 + e_1e_2e'_1 \\ & + c_1c'_1e'_2 - 2c_2c_2e'_2 + 2c_2c'_1e'_2 + e_1c'_1e'_2 + c_1e_2e'_2 + e_1e_2e'_2) \end{aligned}$$

$$p_{10}^* = (-e_{11}c_1c_2 + e_{11}c_1c'_1 + e_{11}c_1e_2 - c_1c_2e'_1 + c_2e'_2c'_1 + c_1c'_1e'_2 + c_1e_2e'_2 - c_1c_2e'_2 + c_1e_2e'_1)/D$$

$$p_{01}^* = (-e_{11}c_1c_2 + e_{11}c_2c'_2 + e_{11}c_2e_1 - c_1c_2e'_1 + c_1e'_1c'_2 + c_2c'_2e'_1 + c_2e_1e'_1 - c_1c_2e'_2 + c_2e_1e'_2)/D$$

$$p_{11}^* = (-c_1c_2(c'_1 + c'_2) + (c_1 + c_2)c'_1c'_2 + c'_1c_2e_1 + c_1c'_2e_2)/D$$

$$\text{Total occupancy} = p^* = p_{01}^* + p_{10}^* + p_{11}^*$$

$$\text{Total occupancy per unit area} = p^* = p_{11}^* + (p_{01}^* + p_{10}^*)/2$$

assess the effect of doubling island size on the presence of a species, per unit sample area. The total probability that a species will be found on the doublet is $P_T = p_{11^*} + p_{10^*} + p_{01^*}$, which of course is greater than p^* .

The full array of transition rates allows one to examine a wide range of assumptions about the consequences of within-island dynamics in colonization and extinction rates, including asymmetrical effects of one island half on the other. It is instructive to consider some special cases. In the following paragraphs, I set $e_{11} = 0$, so that all extinctions are local; this has the effect of allowing the maximal effects of internal spatial dynamics to be observed.

1. A "null" model. If there is no area effect, then the per-unit area rates of colonization and extinction should of course be independent of area, or $c_i = c'_i$ and $e_i = e'_i$. If in addition the island is homogeneous, such that $c_1 = c_2$ and $e_1 = e_2$, it is straightforward to show that $p^* = p'$. Of course, the total probability that a species will be present somewhere on the island is p' on the singlet, and $P_T = p'(2 - p') > p'$ on the doublet.

2. Symmetrical effects on colonization and/or extinction. If the basic colonization rate of each island half is enhanced when the other half is already colonized (as described by the stepping stone and spatial storage effects), and the island is spatially homogeneous, we should have $c_1 = c_2 = c$ and $c'_1 = c'_2 = c'$, with $c < c'$. In like manner, the internal rescue effect in a homogeneous doublet is expressed by $e_1 = e_2 = e$ and $e'_1 = e'_2 = e'$, where $e' < e$.

Figure 4 shows how island area influences local occupancy in the case when local colonization rates are enhanced, but extinction rates are unchanged ($c > c'$, but $e = e'$). We let $c = 1$, which sets the time scale. When $c = c'$ (the dots in the figure), local occupancy on the doublets is identical to that on the singlets. Two simple conclusions emerge from inspection of this figure. First, to observe a strong area effect (on a per-unit area basis) requires high levels of within-island dispersal, compared to the rates of dispersal from outside. Because the curve describing p^* as a function of c'/c is convex, the marginal effect of an increase in internal colonization is greater at lower values for c'/c . Nonetheless, it would appear that to observe a large absolute effect of doubling island size, internal colonization must greatly exceed external colonization. Second, a strong area effect is most likely to be observed at intermediate local extinction rates, roughly comparable in magnitude to the basic colonization rate from the source area. For a numerical example, when $e = c$, a four-fold enhancement of colonization of an empty half by the presence of the population in the other half, increases local occupancy by 43%. By contrast, if $e = c/10$, a similar enhancement in colonization increases occupancy by only 7%. In this case, the species tends to be found everywhere anyway, irrespective of coupling of

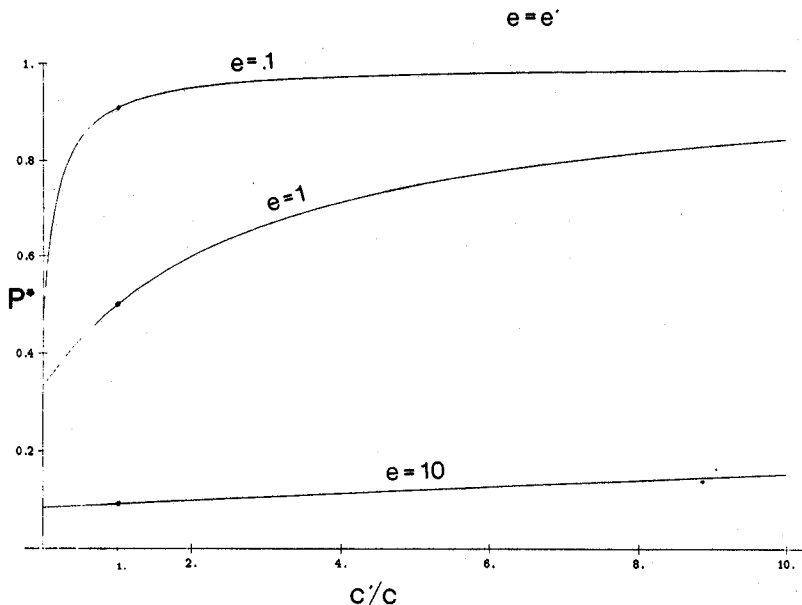


FIG. 4. Patch occupancy curves in a symmetrical model: colonization effect. For three values of the extinction rate, the fraction of randomly chosen island halves that contain the species are shown as increasing functions of c' , the rate of colonization of one half given that the other is already occupied. The time scale is set by $c = 1$.

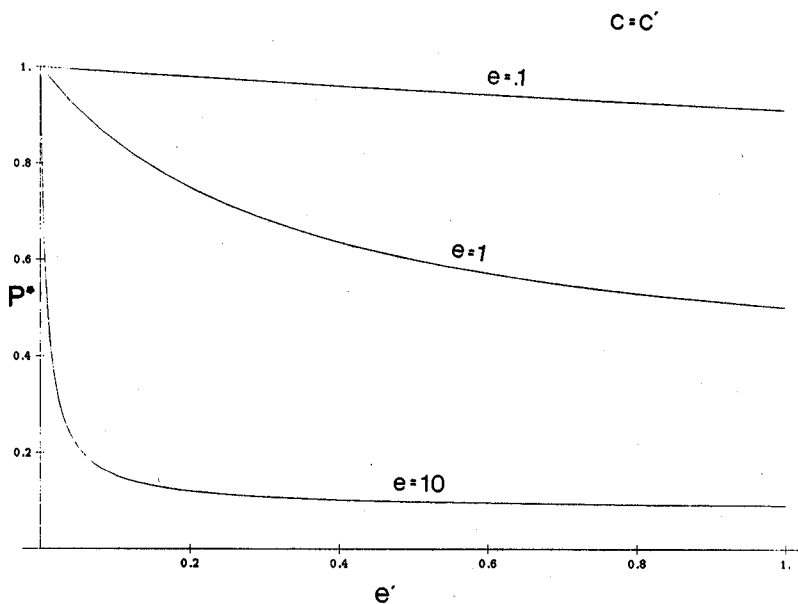


FIG. 5. Patch occupancy curves in a symmetrical model: rescue (extinction) effect. Patch occupancy increases with decreasing e' . $c = 1$.

the two halves by dispersal. If $e = 10c$, the same four-fold enhancement in colonization only increases local occupancy by 24%. This is because extinction occurs so rapidly that a newly founded population on one island half is likely to go extinct before it colonizes the other island half. So the most marked area effects occur when the rate of local extinction approximately matches the rate of long-distance colonization.

An essentially similar conclusion emerges if the only effect of increased island area is via the rescue effect (see Fig. 5). If $e = c$, a decrease in local extinction by a factor of five in one island half (because the adjacent island half is also occupied) substantially increases local occupancy, whereas there is a very slight effect if either $e = c/10$ or $e = 10c$. Because the curve relating p to e' is concave, a very large rescue effect is needed to observe a substantial effect on local occupancy.

The effect of island area on local presence/absence is enhanced if there is simultaneously an increase in the rate of local colonization and a diminution in the rate of local extinction. Figure 6 shows how local occupancy varies jointly as a function of e' and c' , in each case expressed as an order-of-magnitude change from the base colonization and extinction rates. We set the time-scale by allowing $c = 1$ in each case. In Fig. 6a, $e = 10$, and the

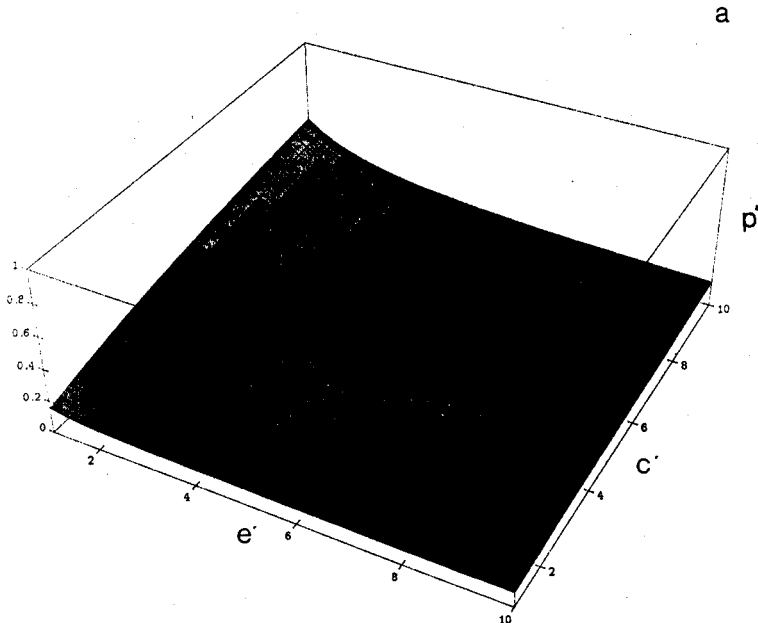


FIG. 6. Patch occupancy as a joint function of c' and e' , for fixed c and e : (a) $c = 1$, $e = 10$. An island effect requires a high c' jointly with low e' ; (b) $c = 1$, $e = 1$. Local occupancy increases more strongly with low c' and e' than in case (a); (c) $c = 1$, $e = 0.1$. Occupancy is largely independent of within-island spatial dynamics.

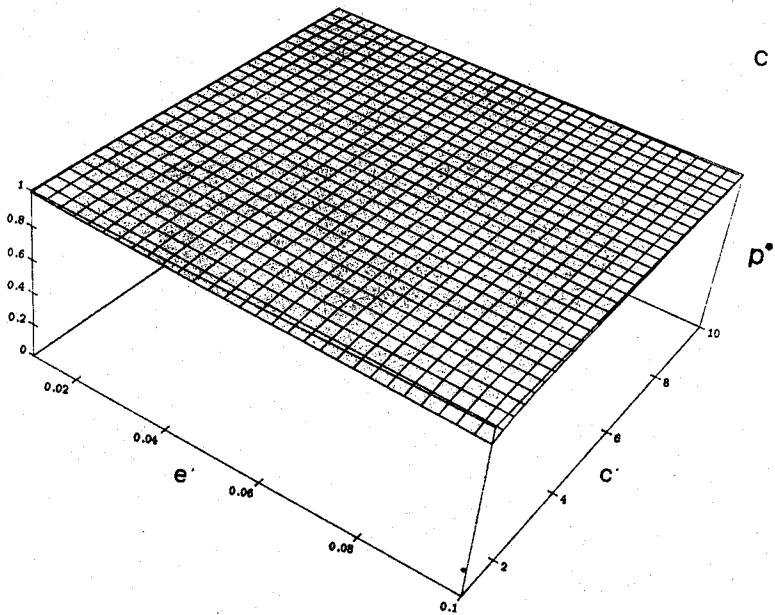
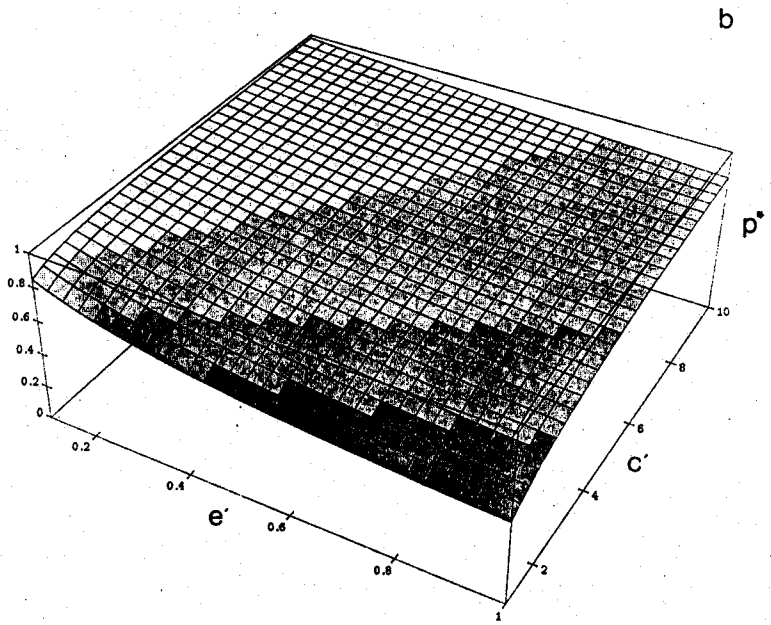


FIG. 6—Continued

equilibrium frequency with which singlets are occupied is $p' = 0.091$. The local occupancy of the doublet is substantially enhanced only if there is spatial coupling that both greatly increases c' and decreases e' . When $e = c = 1$ (Fig. 6b), $p' = 0.5$; smaller changes in these parameters are needed to achieve a given increase in occupancy, though the marginal effect of increased colonization rates tends to exceed that of decreased extinction rates. And finally, when $e = 0.1$, the species is essentially present everywhere, irrespective of local spatial dynamics. Once again, it would appear that area effects are most likely to be observed when local extinction and long-distance colonization rates are roughly equally balanced.

The spatial storage effect and the internal rescue effect are to a degree synergistic. The reason is simply that the opportunity for the internal rescue effect is determined by the size of the pool of doublets in state 11, which in turn directly depends on the magnitude of internal colonization (converting 01 and 10 doublets into 11 doublets).

Figure 7 describes the marginal effect on local occupancy of increased c' and decreased e' , for doublets originally at $c' = c$ and $e' = e$. The marginal effect of increased internal colonization is greatest when both e and c are low, and the marginal effect tends to be larger when e and c are roughly equal in magnitude. The marginal effect of an enhanced internal rescue effect is greatest at low e values; high colonization rates enhance this effect, though to a modest degree. As a concrete example, when $e = e' = 10$ and $c = c' = 1$, $p^* = 0.09$. If either e' is decreased to 2.5, or c' raised to 4, p^* is increased to 0.1129. If both changes are made simultaneously, p^* increases to 0.19, a substantially larger increase in local presence/absence than one would have predicted from a simple additive summation of the effects on colonization and extinction taken separately.

In the introduction to this paper, I speculated that organisms with high rates of within-island dispersal should show substantial area effects, compared to organisms with low within-island dispersal rates. In the parameters of the present model, good within-island dispersal translates into a large c' , and a small e' . Figure 8a shows how the local occupancy of a species with $c' = 10$ and $e' = 0.1$ is strongly enhanced, compared to a singlet, over two orders-of-magnitude variation in c and e . This is particularly noticeable at low c and high e . Figure 8b presents the contrasting case of a species with $c' = 1$ and $e' = 1$; being in a doublet has a trivial effect on the occupancy per unit area of this species.

The above analyses dwell on the properties of a dynamic equilibrium where local colonizations equal local extinctions. The existence of a non-trivial equilibrium depends upon colonization from outside the system. If there is no such colonization, in this model the entire ensemble of local populations inexorably faces extinction. The internal rescue effect and spatial storage effects may nonetheless be of great importance in slowing

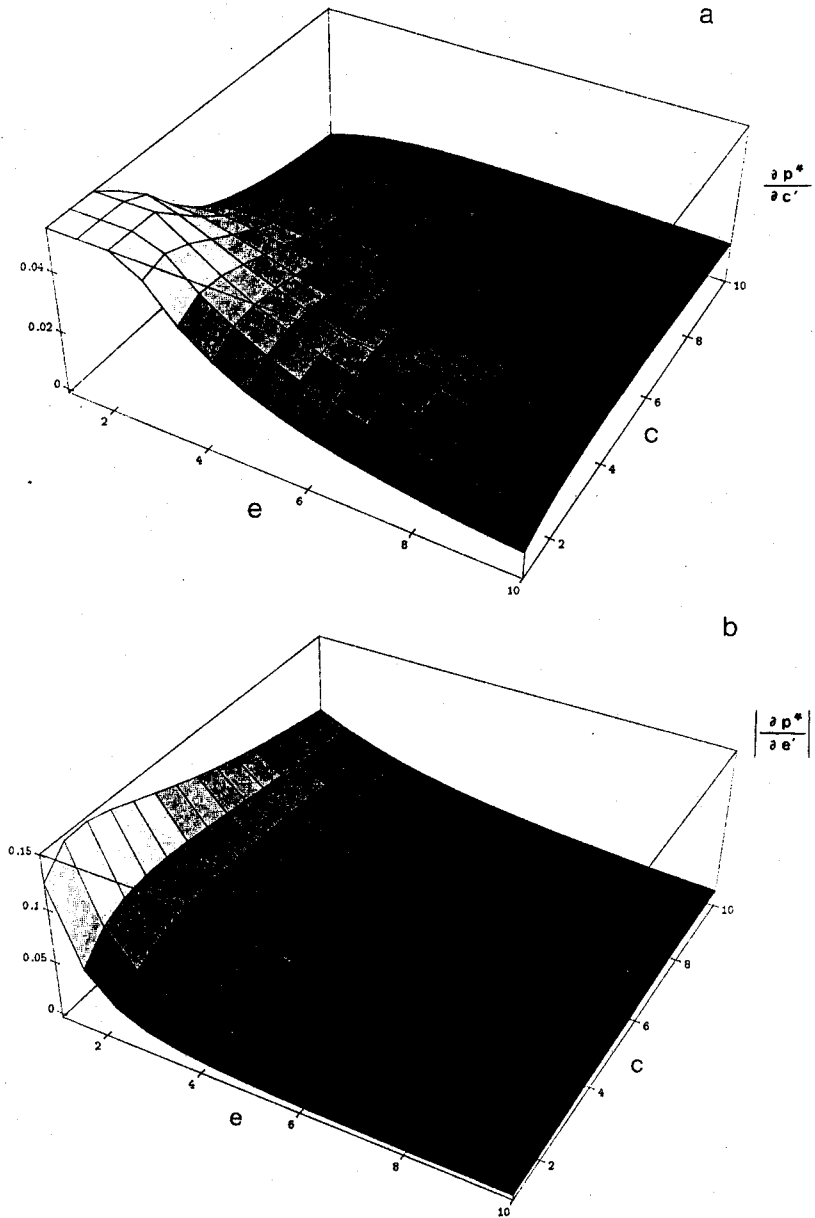


FIG. 7. Sensitivity analyses: (a) The marginal effect on local occupancy of an increase in within-island colonization rates, as a function of e and c ; the partial derivative is evaluated at $c' = c$, $e' = e$. (b) The magnitude of the marginal effect on local occupancy of a decrease in local extinctions due to an internal rescue effect, as a function of e and c , and evaluated at $c' = c$ and $e' = e$.

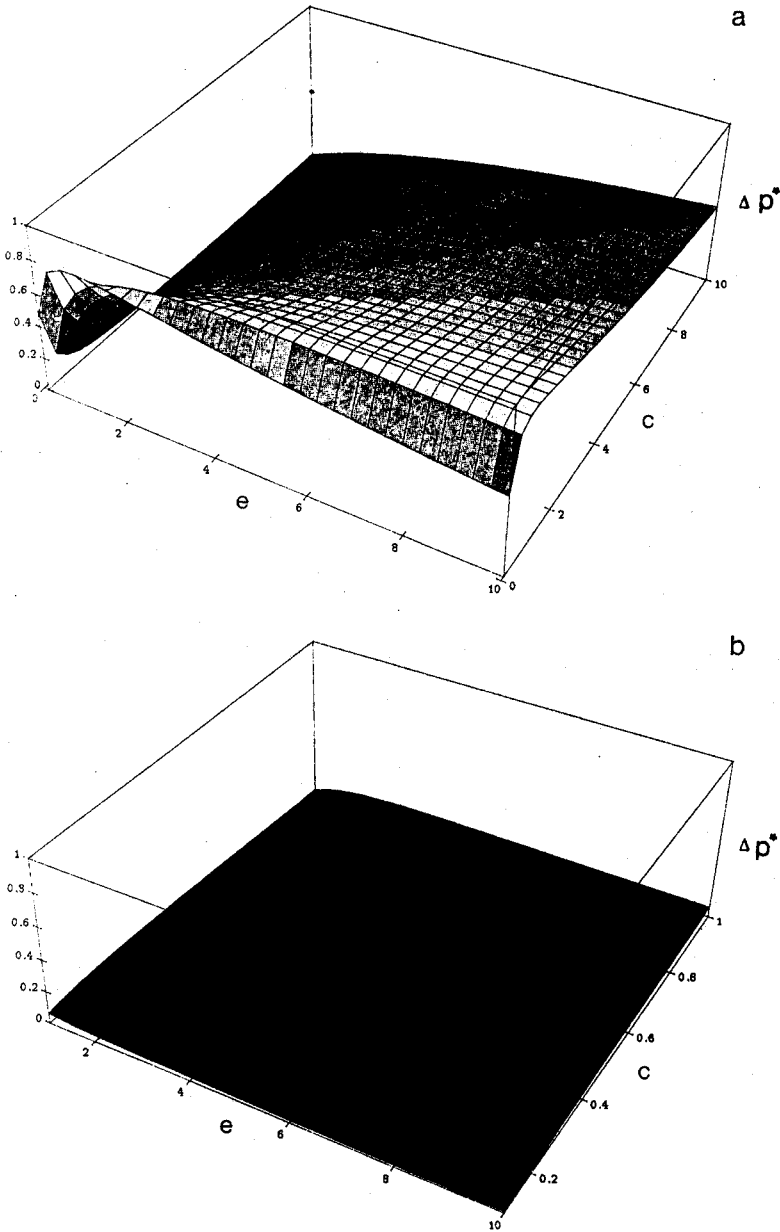


FIG. 8. The effects of within-island dispersal on local occupancy: (a). High-dispersal species, so that $c' = 10$, $e' = 0.1$. The figure shows the increase in occupancy per island half, compared with the null model of $c' = c$, $e' = e$, as a function of the basic colonization and extinction rates, c and e . (b) Low-dispersal species, so that $c' = 1$, $e' = 1$.

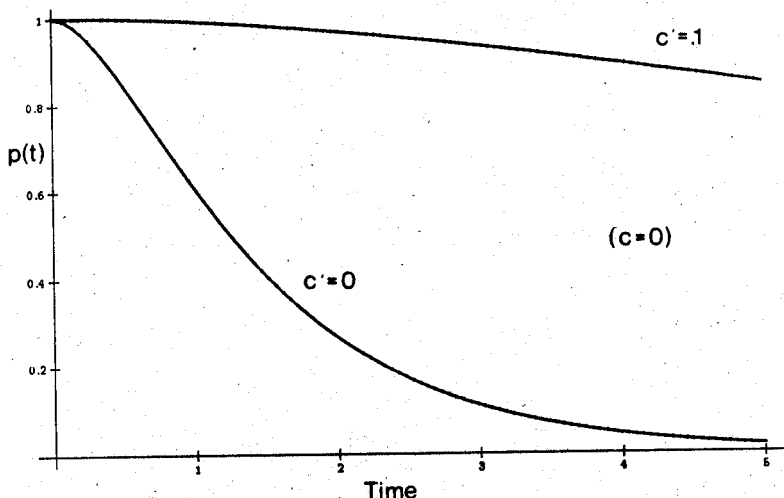


FIG. 9. Non-equilibrium dynamics. The figure depicts total occupancy against time when the rate of external colonization is zero. In the lower curve, the rate of internal colonization is also zero; in the upper curve, this rate is 0.1, and in both curves $e = e' = 1$.

down the rate of population decline. Figure 9 shows one example where a rate of internal colonization that has a negligible effect on the equilibrium occupancy for most rates of external colonization nonetheless substantially brakes the species' decay toward extinction.

As noted above, some organisms do show clear effects of island area at the level of local populations and communities, but others just as clearly do not. The results presented here suggest that one reason for these differences may lie in differences in dispersal biology within islands. For highly mobile animals such as birds, empty pockets on an island can be rapidly colonized, and a steady spillover of individuals from high to low density areas may greatly reduce the chance of local extinction. For such species the entire island in effect harbors a single population, and the standard demographic models of population persistence based on aggregate population parameters should apply. But for many groups of organisms, such as heavy-seeded plants, snails, and soil organisms, mobility within even a modest-sized island may be quite low. For these species, it makes sense to envisage all but very small islands to be metapopulations of local populations coupled by limited dispersal. Islands of different size in this perspective amount to metapopulations with differing numbers of constituent subpopulations. [Because islands experience colonization from outside, one might dub such metapopulations "open metapopulations."] The "doublet" model analyzed above suggests that area effects in such metapopulations, if they are seen at all, may hinge on a rather fine balance between rates of

local colonization and extinction. I should emphasize that this conclusion is based on a very simple spatial structure, and that more work needs to be done on more complex spatial arrays to gauge the generality of this idea. A broader conclusion is that a fruitful direction of research should be the application of contemporary patch dynamic theory to classic island biogeographic questions and systems.

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