

The distribution and abundance of populations limited at multiple spatial scales

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Summary

1. We use mathematical programming to explore long-term equilibrium population distribution and abundance effects arising from a single-patch reaction–diffusion model when ecological factors limit carrying capacity at two different spatial scales. Both homogeneous and heterogeneous habitat patches are investigated under passive diffusion conditions. Capacity limits, reproduction and dispersal rates, and habitat preferences are individually varied.
2. When landscape-scale habitat factors are strongly limiting, and reproduction and dispersal processes are less so, suitable population arrangements can be either clustered or highly fragmented.
3. Population clustering also occurs when strong habitat preferences are introduced, even though few members of the clusters may actually occupy the preferred sites.
4. As reproduction or dispersal rates become increasingly limiting in the system (i.e. as the parameters approach extinction thresholds), population clustering within a habitat patch is required to reach long-term equilibrium population levels.
5. These results offer a potential explanation for why species–habitat association studies have been characterized by high variability.

Key-words: carrying capacity, habitat association, mathematical programming, population contiguity and fragmentation, reaction–diffusion.

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Introduction

Although carrying capacity is often modelled for single populations as a simple equilibrium or saturation point, the concept is widely recognized as being more complex (Dhondt 1988). For more than a century, biogeographers have recognized that population distributions tend to be limited by a multitude of factors (Haeckel 1866; Shelford 1911; Udvardy 1969). These factors also affect population abundance, and can affect populations at different spatial scales (Morris 1987; Levin 1992); for example, many species forage over spatially extensive areas, but reproduce in specific locales because of obligate relationships with habitat characteristics that occur sporadically across a landscape (Orians & Wittenberger 1991). Under such circumstances,

populations can be limited at micro-scales by the availability of suitable breeding sites, and at macro-scales by food availability. Similar instances of multi-scale population limitation are found in predator–prey systems where species can be limited broadly by wide-ranging predators, or locally by the availability of breeding sites (Henschel & Lubin 1997). Less familiar examples can be found among species characterized by multi-phase life cycles; for example, many adult forms of marine intertidal organisms are sessile and subject to population limitations stemming from the local availability of suitable substrate. Conversely, the larval phase of these species is often highly mobile, distributed diffusely throughout the marine environment, and subject to large-scale limitations caused by nutrient availability, predation or weather events (Roughgarden, Gaines & Possingham 1988). Indeed, there is a general recognition that observed population distribution and abundance patterns result from limitations at several spatial scales. As Levin (1992, p. 1943) puts it, ‘in some cases, the patterns must be under-

stood as emerging from the collective behaviours of large ensembles of smaller scale units. In other cases, the pattern is imposed by larger scale constraints.' This study focuses on the combined effect of such multi-scale limitations.

Ecological adaptations to multi-scale influences on populations are numerous (Hengeveld 1987; Menge & Olson 1990), resulting in a variety of distinct simulation approaches for particular populations. Given this variation, general theoretical treatment of how multi-scale limiting factors can affect population distribution and abundance should be useful. This paper reports the results of an investigation of combined micro- and macro-scale limiting factor effects within a spatial optimization analysis framework (Hof & Bevers 1998). Mathematical programming (see Luenberger 1984; Bazaraa, Jarvis & Sherali 1990) and reaction-diffusion modelling (see Okubo 1980; Holmes *et al.* 1994; Bevers & Flather 1999) are used to explore these effects for a theoretical population randomly dispersing throughout a single patch of habitat.

In a study of habitat design using similar methods (Bevers *et al.* 1997) a fragmented population was observed as an unanticipated optimal solution, while in other work (Bevers & Flather 1999) population arrangements converged to contiguous Gaussian-like spatial distributions of abundance near extinction thresholds. These observations led us to hypothesize that multi-scale limiting factors will allow fragmented populations to occur under a broad set of reaction-diffusion parameters, converging toward Gaussian-like population clusters as critical thresholds are approached. We further examine population clustering in heterogeneous habitat by imposing local habitat preferences within a patch.

Methods

REACTION-DIFFUSION

Allen (1987; following Levin 1974) describes a multi-dimensional random walk reaction-diffusion model for a fragmented complex of N habitat patches as:

$$dv_i/dt = v_i f_i(v_i) + \sum_{j=0}^N D_{ij}(v_j - v_i); i = 1, N \quad \text{eqn 1}$$

$$D_{ij} = D_{ji} \geq 0 \quad \forall i, j$$

$$v_0 = 0$$

where v_i is the adult population in patch i as a function of time t , and $f_i(v_i)$ is the per capita rate of reproduction (net of mortality unassociated with dispersal, as discussed below). D_{ij} is a patch-to-patch passive diffusivity constant that determines

the net patch i population gain from (or loss to) patch j based on the difference between the patch populations. Nonhabitat is indexed by $j = 0$. In this model, dispersing organisms can successfully traverse regions of nonhabitat, but some of them perish and are treated as dispersers into nonhabitat. The nonhabitat population v_0 is fixed at zero so that D_{i0} times $-v_i$ defines a population loss as a result of unsuccessful dispersal from any patch i . The habitat complex comprises those patches (indexed by i) which are 'connected' by positive diffusivity ($D_{ij} > 0$) with at least one other patch (some $j \neq i > 0$). Bevers & Flather (1999) show that by letting i and j index cells that represent breeding sites instead of patches, equation 1 becomes suitable for examining intra- as well as interpatch population distribution and abundance. In this study, we use a 13×13 block of square cells to represent 169 breeding sites in a single habitat patch.

Reproduction and dispersal are modelled as simultaneous processes in equation 1, so that reproduction in each cell can implicitly contribute to the diffusion summation term. In this unstructured model only adults and offspring are distinguishable, and four cases are possible: only adults disperse; only juveniles disperse; adults and juveniles disperse identically; or adults and juveniles disperse, but not identically (see Bevers & Flather 1999). For simplicity, we assume that reproduction occurs at a constant per capita rate (i.e. $f_i(v_i) = r$ for all i) and that adults and juveniles disperse identically.

To estimate cell-to-cell dispersal, it is useful to define a new parameter g_{ij} as the proportion of organisms from cell i expected to disperse to cell j (by any of many routes) per unit of time. With adults and juveniles dispersing identically, all diffusivity constants D_{ij} are equal to $[1 + r] g_{ij}$. Again for simplicity, we assume identical diffusion from each cell in the patch, calculated in the following manner. Organisms disperse, on average, from the centre of each cell outward in uniformly random directions. Dispersal probabilities decline with distance (x) according to:

$$p_x(x) = \mu^{-1} \exp [-(x-\theta)/\mu]; x > \theta, \mu > 0$$

as defined by a mean dispersal distance (μ) from the centre of the home cell, using a minimum dispersal distance (θ) of zero. Diffusion proportions (g_{ij}) are estimated by numerical approximation over distances and angles defined by the boundaries of each destination cell (indexed by j) relative to the centre of each source cell (indexed by i). Using an exponential distribution for dispersal distance (as in Fahrig 1992) results in a globally connected cellular lattice.

MULTI-SCALE LIMITING FACTORS

We wish to represent a micro-scale limit such as breeding site capacity, and a macro-scale limit such as a predation effect in a general way. Our two spatial scales are the cells and the patch. To apply a micro-scale capacity limit, we add to the model a set of constraints limiting the adult population in each cell:

$$v_i \leq b_i \quad \forall i. \quad \text{eqn 2}$$

For most of our analyses a homogeneous patch is assumed, and the cellular breeding site capacity parameter b_i is set to a scale value of 1.0 population unit for all cells. To apply a macro-scale capacity, another constraint limiting total patch population is added to the model:

$$\sum_i v_i \leq C \quad \text{eqn 3}$$

where C is the landscape level or total patch capacity.

The generality and simplicity of equations 1–3 eliminate many ecological details from the model: for example, our use of fixed cell sizes combined with equation 2 disregards fluctuation in territory sizes, the possibility of overpopulation, or cell occupancy by nonbreeding adults. Instead, any surplus cellular population is presumed to perish, and all adults are assumed to reproduce. Our use of a constant r -value for reproduction in equation 1 is consistent with that, but is simplistic as well. Combined with our choice of diffusion parameters, these assumptions are not unreasonable however, producing a probability of dispersers surviving that is proportional to the amount of unoccupied habitat surrounding a given cell, with distance decay. Similarly, equation 3 ensures that any surplus patch population also perishes as a result of a macro-scale limiting factor. Using this approach we can focus on identifying the range of suitable population arrangements without having to specify the behavioural or energetic mechanisms underlying the limiting factors. The effects of such mechanisms are considered in the Discussion.

MATHEMATICAL PROGRAMMING

Model population distribution and abundance under equilibrium conditions can be observed by setting the rates of change (the dv_i/dt terms in eqn 1) to zero and maximizing total population with equations 1–3 as constraints. We recognize that random perturbations can disrupt any balance in the system causing a continuing sequence of disequilibria. Nonetheless, we are interested in equilibrium states because in the aggregate those that maximize total population form the attractors (Çambel 1993) towards which the system tends to move after being

perturbed (Cushing *et al.* 1998). Mathematical programming provides a convenient method for finding those attractors.

Because a variety of maximal equilibria may exist for our 13×13 cell patch under any given set of parameter values, a systematic approach is needed to explore the possible population arrangements. Our approach involves solving the model (eqns 1,2,3) with four different objective functions: CNTR, EDGE, FRAG and EVEN (defined below). Each of these objective functions allows us systematically to search for extreme distribution and abundance patterns while maintaining maximum equilibrium population conditions for a given set of parameter values. Following a preliminary optimization using:

$$\text{Maximize : } \sum_{i=1}^N v_i \quad \text{eqn 4}$$

with equations 1–3 as constraints to identify the maximum equilibrium population, we convert the landscape-level capacity constraint (eqn 3) to an equality constraint and set that right-hand side (C) to the new equilibrium population level just determined, forcing the model to maintain it. We then re-optimize the problem four more times, replacing equation 4 with a different distribution-favouring objective function each time.

In our 13×13 patch, the CNTR objective encourages high population densities in the centre of the patch by maximizing a weighted sum of the cellular populations:

$$\text{Maximize : } \sum_{i=1}^N w_i v_i \quad \text{eqn 5}$$

with the greatest weight placed on the centre cell ($w_{85} = 1.0$, with cells indexed from the upper left corner). Each of the adjacent cells forming a concentric square around the centre cell is weighted 10 times less, and so on to the outermost cells, which are each weighted 1.0×10^{-6} . The EDGE maximization objective function is weighted in the opposite manner to encourage high population densities along the edge of the complex, with the centre cell weighted at 1.0 and the outermost cells each weighted at 1.0×10^{-6} . The FRAG maximization objective function encourages hyperdispersion of cellular populations, with weights of 1.0 for each of the 36 cells occurring in both even-numbered rows and columns in the complex (so that none of these 36 cells adjoin). Cells with odd-numbered rows or columns, but not both, directly facing those 36 cells are assigned weights of -1.0×10^{-6} . Cells with both odd-numbered rows and columns diagonal to the 36 positively weighted cells are assigned weights of -1.0×10^{-3} . The EVEN objective function uses a min-max (Luce & Raiffa 1957) formulation (eqn 6) to

encourage evenly distributed equilibrium cellular populations:

Minimize: λ eqn 6

subject to: $\lambda \geq v_i \forall i$

where the largest equilibrium cellular population (λ) is minimized.

When only a single distribution and abundance pattern maximizes the total population, all four of these objective functions will be forced to produce the same equilibrium population arrangement. Conversely, solutions from our four objective functions will be different when there is flexibility in how populations can be arranged on the landscape (i.e. multiple equilibria exist that can support the same total population). For each solution from the above objective functions, we calculate a pair of contiguity measures (Geary 1954; Dacey 1968) to describe the degree to which population distribution is clustered (referred to as z_{11}) and abundance is concentrated (referred to as K) on the landscape (see Appendix for definition and interpretation of these measures).

Results

We begin by examining equilibrium population distributions for a homogeneous habitat patch 13×13 units of distance in size, so that each cell measures one distance unit per side. Cellular population capacities (b_i) are set to 1.0 (perhaps representing many

organisms) for all 169 cells. The net reproduction rate (r) is set to 0.85, and mean dispersal distance (μ) is set to 2.5 units of distance. This set of values represents our base parameter settings. Figure 1 shows two of several alternative equilibrium population distributions found by random trials with the patch-wide capacity (C) set to 36 population units. While both maps exhibit substantial clustering ($z_{11} > 3.31$), it is clear from Fig. 1a that small, relatively isolated cellular populations can occur under equilibrium conditions. Figure 1a also shows a more concentrated pattern of abundance ($K = 0.57$), while Fig. 1b displays a more even abundance ($K = 0.27$), resulting from substantially fewer unoccupied cells.

Despite the similarities and differences between Fig. 1a,b, inferences are difficult without more systematic analysis. At these parameter settings, the objective function (eqn 4) is limited to a total equilibrium population of 36 by the complex-wide capacity constraint (eqn 3). To examine the flexibility possible in equilibrium population arrangements, we converted equation 3 to an equality constraint with C set to 36 and replaced equation 4 with the CNTR, EDGE, FRAG and EVEN objective functions (one at a time). The resulting population arrangements (still at equilibrium levels of 36) are shown for these objective functions in Fig. 2a-d, respectively. Each of these figures portrays one solution from a small family of possible arrangements that vary little (e.g. mirror images are always alternative solutions for our symmetric landscape).

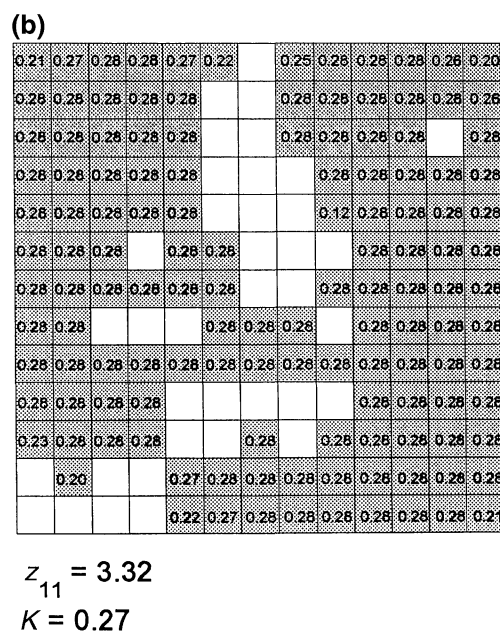
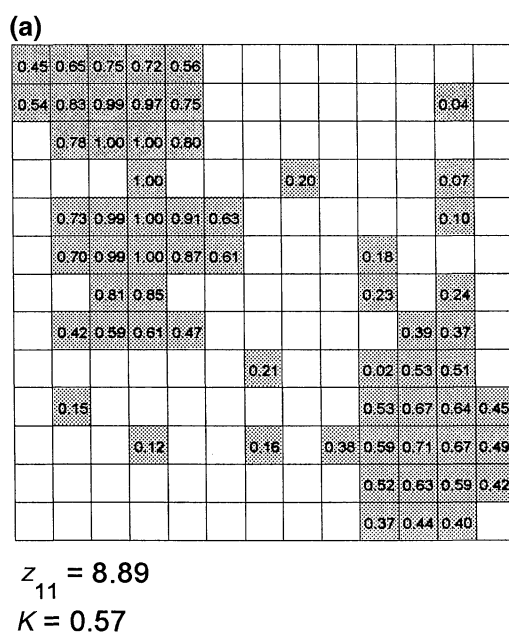


Fig. 1. Two of many possible equilibrium population arrangements in a 13×13 cell habitat patch with parameter settings $C = 36$, $r = 0.85$, $\mu = 2.5$ and all $b_i = 1.0$.

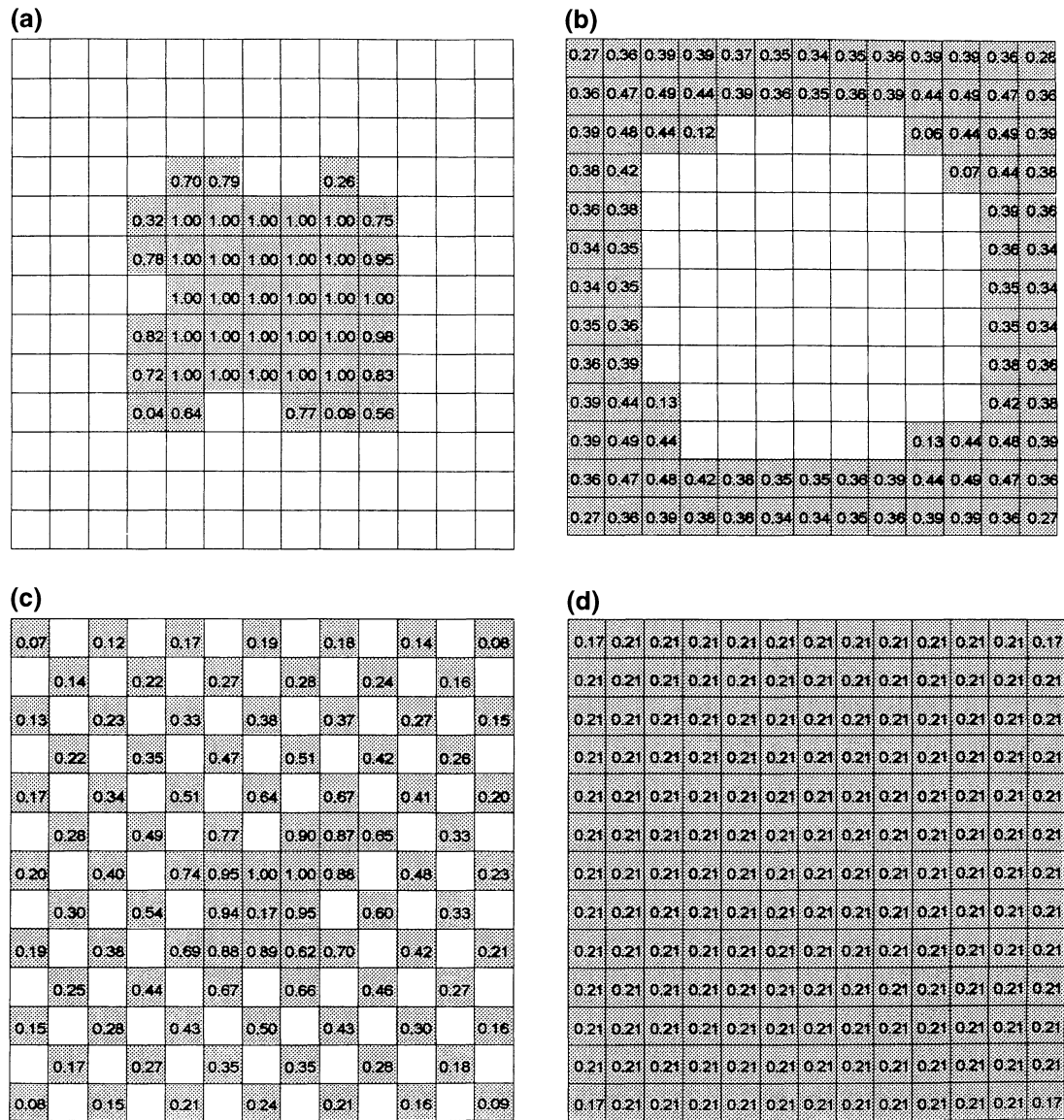


Fig. 2. Equilibrium population arrangements in a 13 × 13 cell habitat patch with parameter settings $C = 36$, $r = 0.85$, $\mu = 2.5$ and all $b_i = 1.0$ for the (a) CNTR, (b) EDGE, (c) FRAG, and (d) EVEN objective functions.

The reaction–diffusion constraint (eqn 1) appears to have little effect on the CNTR objective function results. The central 25 cells are fully populated and the remaining 11 population units are arranged more or less haphazardly around the next concentric layer of cells. Equation 1 does appear to have some effect, however, with the EDGE objective function. Instead of placing all 36 population units in the outermost set of cells, the equilibrium population is distributed throughout the two outer concentric squares, as well as in the corners of the next ring inward. The model is apparently unable to populate the edge of the complex densely without some connecting cellular populations toward the interior. Similarly, the FRAG objective function results show that the 36 positively weighted (hyperdispersed) cells

cannot be used to contain all 36 population units given passive reaction–diffusion processes at these parameter settings. All of the diagonally adjoining cells are populated despite negative weights in the objective function. Six of the adjacent cells near the centre of the complex are populated despite very negative weights in the objective function. The EVEN objective function results, on the other hand, appear to be largely unconstrained by reaction–diffusion processes, similar to the CNTR objective function results. Only the four corner cells of the complex are affected in this case. Contiguity statistics for these results are reported in the first line of Table 1. Overall, the model appears to have a large degree of flexibility in equilibrium population arrangement at these parameter settings, although

Table 1. Contiguity statistics for population distribution (z_{11}) and concentration (K) under the CNTR, EDGE, FRAG and EVEN objective functions for a 13×13 cell habitat patch with base parameter settings $C = 36$, $r = 0.85$, $\mu = 2.5$ and all $b_i = 1.0$, and for individual changes to those parameter settings

Parametric change	CNTR		EDGE		FRAG		EVEN	
	z_{11}	K	z_{11}	K	z_{11}	K	z_{11}	K
None (base)	18.45	0.857	8.54	0.371	-0.01	0.396	†	0.213
$r = 0.5276$	19.34	0.750	7.42	0.279	1.87	0.364	†	0.213
$r = 0.20515$	†	0.213	†	0.213	†	0.213	†	0.213
$\mu = 4.7661$	18.52	0.468	5.66	0.250	3.55	0.327	†	0.213
$\mu = 7.0322$	†	0.213	†	0.213	†	0.213	†	0.213
$b_{85} = 2.0$	19.72	0.942	8.56	0.375	0.12	0.391	‡	‡
$v_{85} \geq 1.0$	19.72	0.942	4.49	0.359	0.12	0.391	‡	‡
$v_{85} \geq 1.5721$	19.72	0.942	18.95	0.918	19.60	0.918	‡	‡

†The distribution statistic (z_{11}) cannot be computed when all cells in the complex are occupied.

‡The minimax form of the EVEN objective function can be ineffective when a lower bound is placed on some v_i , so no results are reported.

that flexibility is somewhat restricted. Because of reaction–diffusion constraints, some amount of clustering seems unavoidable in all of these solutions, but the clusters are not necessarily prominent (e.g. Fig. 2c).

REPRODUCTION AND DISPERSAL EFFECTS

Our hypothesis regarding multi-scale limiting factor effects on population fragmentation and clustering hinges on the notion of critical extinction thresholds in reaction–diffusion systems. Skellam (1951) and others have demonstrated with continuous space and time models that for theoretical populations following passive diffusion processes in a single patch of homogeneous habitat a critical patch size generally exists, below which extinction is expected. Critical extinction thresholds also exist in discrete models such as ours (Bevers & Flather 1999; see also Lande 1987; Pagel & Payne 1996 for related demographic equilibrium extinction thresholds). In our model, this threshold is defined by the combination of habitat size and shape, the intrinsic rate of population growth (r), and mean dispersal distance (μ , hence all g_{ij}). By varying one of these parameters and holding the others constant, a critical set of threshold values for all parameters can be determined. Below the threshold point, the optimization model in equations 1–4 is unable to produce any expected equilibrium population for the patch (i.e. eqn 4 is maximized at zero, implying extinction). For a given habitat patch, decreasing r or increasing μ tends to push the equilibrium population towards (or below) extinction threshold conditions. Thus, we can investigate more restrictive reaction–diffusion systems by decreasing r or increasing μ in our model and comparing the resulting spatial arrangements with the solutions from less restrictive parameter settings.

Returning to our base parameter settings with $C = 36$, all $b_i = 1.0$, $\mu = 2.5$ and $r = 0.85$, we decrease the net reproduction rate r -value until we identify an extinction threshold at $r = 0.20515$ (the artificially high precision here simply reflects the nature of mathematical thresholds). With the r -value set to 0.20514 or less, equation 4 is maximized at zero. Conversely, with the r -value set to 0.20515, equation 4 is maximized at a total equilibrium population of 36 units because the complex-wide capacity constraint (eqn 3) is simultaneously limiting. With equation 3 converted to an equality constraint at $C = 36$, the CNTR, EDGE, FRAG and EVEN objective functions (as well as eqn 4) all produce identical Gaussian-like equilibrium population distributions (Fig. 3). No latitude exists in how the

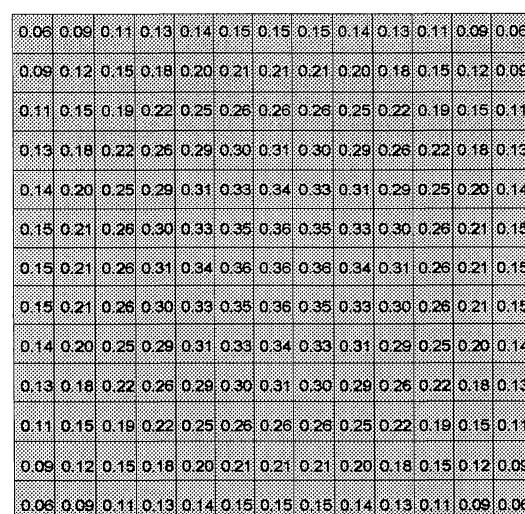


Fig. 3. Equilibrium population arrangements in a 13×13 cell habitat patch near extinction threshold conditions with parameter settings $C = 36$, $r = 0.20515$, $\mu = 2.5$ and all $b_i = 1.0$ for all objective functions.

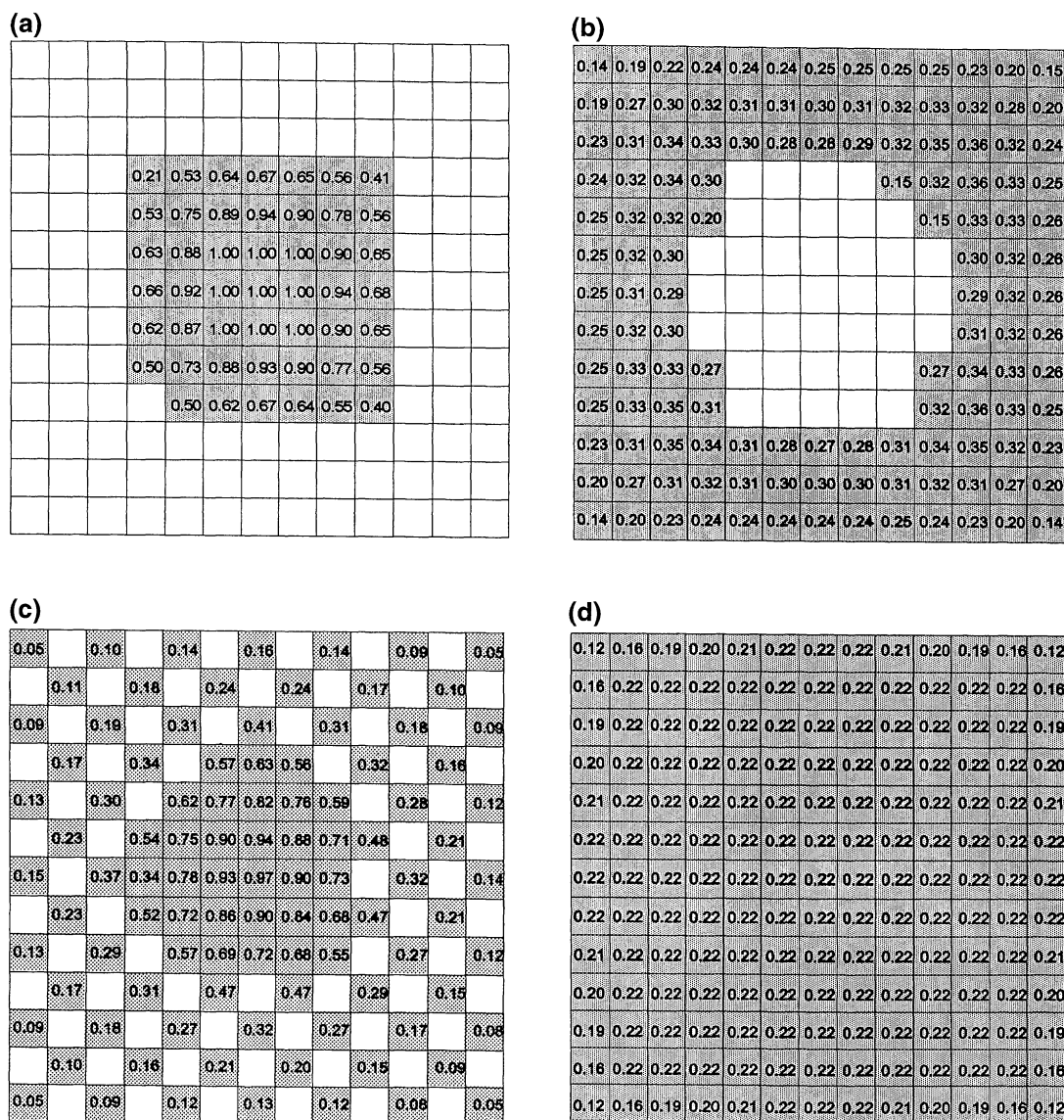


Fig. 4. Equilibrium population arrangements in a 13×13 cell habitat patch with net reproduction $r = 0.5276$ [approximately midway between initial settings (Fig. 2) and extinction threshold conditions (Fig. 3)] and unchanged values for all other parameters ($C = 36$, $\mu = 2.5$ and all $b_i = 1.0$) for the (a) CNTR, (b) EDGE, (c) FRAG, and (d) EVEN objective functions.

equilibrium population can be arranged when near extinction conditions, and our contiguity indices are invariant (Table 1).

At $r = 0.5276$, about midway between our original r -value and the extinction threshold r -value, equilibrium arrangements from the CNTR, EDGE, FRAG and EVEN objective functions (Fig. 4a–d) appear to be intermediate in flexibility (compare with Fig. 2a–d and Fig. 3). This reduction in suitable arrangements does not, however, appear to have been halved. As shown in Table 1, with this r -value we observe population clustering for the CNTR, EDGE and EVEN objective functions comparable to the results from our base parameter settings, but

with slightly lower concentrations. Population contiguity under the FRAG objective function deviates from the base results because the more restrictive reaction–diffusion system forces more of the population towards the centre of the complex (see Fig. 4c).

Returning again to our base parameter settings with $C = 36$, all $b_i = 1.0$, $r = 0.85$ and $\mu = 2.5$, we next increase the mean dispersal distance μ until we identify another extinction threshold at $\mu = 7.0322$. Again, the resulting equilibrium population is 36 because the complex-wide capacity constraint (eqn 3) and the reaction–diffusion constraints (eqn 1) are simultaneously limiting. As with a critical r -value, all of the objective functions produce identical

0.10	0.12	0.14	0.15	0.16	0.17	0.17	0.17	0.16	0.15	0.14	0.12	0.10
0.12	0.15	0.17	0.19	0.20	0.21	0.21	0.21	0.20	0.19	0.17	0.15	0.12
0.14	0.17	0.20	0.22	0.24	0.25	0.25	0.25	0.24	0.22	0.20	0.17	0.14
0.15	0.19	0.22	0.25	0.26	0.27	0.28	0.27	0.26	0.25	0.22	0.19	0.15
0.16	0.20	0.24	0.26	0.28	0.29	0.30	0.29	0.28	0.26	0.24	0.20	0.16
0.17	0.21	0.25	0.27	0.29	0.30	0.31	0.30	0.29	0.27	0.25	0.21	0.17
0.17	0.21	0.25	0.28	0.30	0.31	0.31	0.31	0.30	0.28	0.25	0.21	0.17
0.17	0.21	0.25	0.27	0.29	0.30	0.31	0.30	0.29	0.27	0.25	0.21	0.17
0.16	0.20	0.24	0.26	0.28	0.29	0.30	0.29	0.28	0.26	0.24	0.20	0.16
0.15	0.19	0.22	0.25	0.26	0.27	0.28	0.27	0.26	0.25	0.22	0.19	0.15
0.14	0.17	0.20	0.22	0.24	0.25	0.25	0.25	0.24	0.22	0.20	0.17	0.14
0.12	0.15	0.17	0.19	0.20	0.21	0.21	0.21	0.20	0.19	0.17	0.15	0.12
0.10	0.12	0.14	0.15	0.16	0.17	0.17	0.17	0.16	0.15	0.14	0.12	0.10

Fig. 5. Equilibrium population arrangements in a 13×13 cell habitat patch near extinction threshold conditions with parameter settings $C = 36$, $r = 0.85$, $\mu = 7.0322$ and all $b_i = 1.0$ for all objective functions.

equilibrium population distributions (Fig. 5), and no latitude in arrangement exists. Considered as a three-dimensional graph, Fig. 5 is only slightly flatter than Fig. 3 despite much more equitable dispersal probabilities between cells. Setting μ midway between our initial value and the extinction threshold value produces a set of responses similar to Fig. 4, for which an intermediate r -value was used. Changes in contiguity statistics are similar to those observed when we let r approach an extinction threshold, except that we observe greater population clustering for intermediate values of μ under the FRAG objective function (Table 1). This suggests that the population becomes somewhat less tolerant of fragmented arrangements as μ approaches an extinction threshold, relative to r .

HETEROGENEOUS HABITAT EFFECTS

In our investigations so far, we have considered only homogeneous habitat patches (all $b_i = 1.0$). Our observations that flexibility in equilibrium population distribution and abundance decreases as reaction-diffusion processes approach extinction threshold conditions could be an artefact of using a simple homogeneous environment. To explore possible contiguity effects in a heterogeneous environment, we increase the saturation capacity of just the centre cell in our 13×13 cell patch from one population unit to two ($b_{85} = 2.0$). One set of results from maximizing equation 4 with $C = 36$, all other $b_i = 1.0$, $r = 0.85$ and $\mu = 2.5$ is shown in Fig. 6(a), although many equilibrium distributions are possible (contiguity statistics for the CNTR, EDGE,

FRAG and EVEN objective functions are reported in Table 1). The distribution in Fig. 6(a) is noteworthy, however, because no equilibrium population occurs in the centre cell. Without behavioural or energetic mechanisms in the model, passive reaction-diffusion (eqn 1) does not necessarily cause the solution to exploit the higher quality habitat represented by increases in breeding site capacity. Some form of preferential habitat selection has to be included in the model if we want equilibrium populations to occupy (prefer) certain habitat areas.

Biasing dispersal probabilities to produce lower emigration rates from some sites would be a reasonable way to model preferential habitat selection, but would also cause the results to be less comparable with our previous experiments. Without deviating from passive diffusion, a simple way to model cellular preferences is to place lower bounds on the cellular population (v_i) variables, requiring some population to occupy those cells. Small lower bounds close to zero imply weak habitat preferences. Large lower bounds close to saturation capacity (b_i) imply stronger habitat preferences. Figure 6b shows one arrangement resulting from setting a lower bound of one unit on the population in the centre cell ($1 \leq v_{85} \leq b_{85}$, with b_{85} still set to 2). Like Figure 6a, some clustering is evident, but several cellular populations remain relatively small and isolated. Although all equilibrium populations now include a population of at least one unit in the centre cell, many alternative distributions are still possible, and most population contiguity measures are identical to the case with no preferential habitat selection (Table 1). The EDGE objective function is the one exception. Two population clusters occur rather than one, causing a large drop in z_{11} , because the lower bound restriction on v_{85} forces some population in and around the centre cell while the objective function locates the remaining population around the edge of the complex.

As we increase the lower bound on the equilibrium population in the centre cell, population arrangement alternatives decrease until, at a lower bound of 1.5721 units (Fig. 6c), little flexibility is left. All objective functions show high contiguity statistics as the population clusters around the preferred habitat (Table 1). Given the other parameter settings, it is impossible to increase v_{85} further, even though the cellular capacity limit has not been reached ($v_{85} \text{ max} = 1.5721 < b_{85} = 2$). The reaction-diffusion constraints (eqn 1) are strongly limiting, forcing the entire equilibrium population to cluster around the centre cell in order to support the largest population possible in the preferred cell under the circumstances.

To test for this effect at the edge of the habitat patch, we reset the lower bound on the population in the centre cell back to zero, and gradually

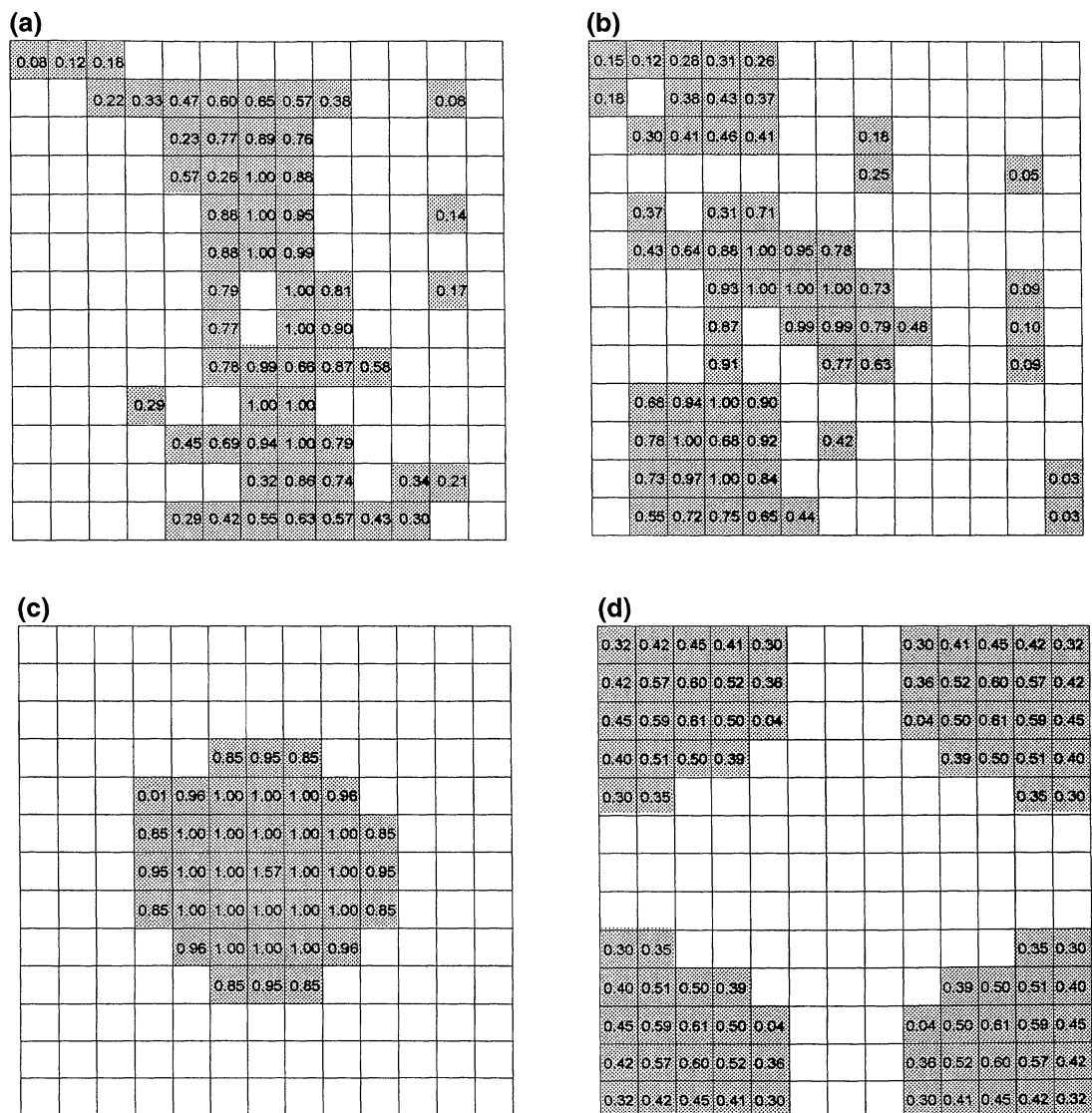


Fig. 6. Example equilibrium population arrangements in a 13×13 cell heterogeneous habitat patch with parameter settings $C = 36$, $r = 0.85$, $\mu = 2.5$, $b_{85} = 2.0$ and all other $b_i = 1.0$ given (a) no habitat preferences (i.e. lower bounds of zero for all v_i), (b) moderate preference for the centre cell ($v_{85} \geq 1.0$), (c) strong preference for the centre cell ($v_{85} \geq 1.5721$), and (d) strong preference for the four corner cells ($v_1, v_{13}, v_{157}, v_{169} \geq 0.3184$).

increased lower bounds identically for the populations in the four corner cells of the complex ($v_1, v_{13}, v_{157}, v_{169}$). At lower bound values of 0.3184 for each of the four cells, highly clustered equilibrium populations again result (Fig. 6d) with no further gain possible.

Discussion

Distribution and abundance patterns across a habitat complex are fundamentally influenced by how individuals within a population move and reproduce, and by other factors limiting populations at various scales. We have represented population growth and movement with a simple reaction-diffu-

sion formulation that models dispersal passively with distance decay across a lattice of breeding sites. Overlaying this reaction-diffusion process is a set of carrying capacity constraints at both the habitat cell scale (e.g. a breeding adult limit within each site) and the landscape scale (e.g. a predation effect limit). Mathematical programming was used to examine distribution and abundance patterns that achieve maximum equilibrium population conditions within a habitat patch subject to reaction-diffusion and carrying capacity constraints. The results from our experiments provide several new insights regarding the interpretation of population distribution and abundance patterns.

In all of our experiments, we observed that when a landscape-level carrying capacity constraint (eqn 3) is strongly limiting and reaction–diffusion (eqn 1) is less so, then many equally ‘good’ (i.e. supporting the same total population) equilibrium population distributions with varying degrees of fragmentation are possible. This flexibility is inferred from the fact that we were able to demonstrate a broad range of distributions that showed both clustering and fragmentation (Figs 1, 2). Conversely, as reaction–diffusion processes become more limiting, possible population arrangements become more restrictive. Under strong reaction–diffusion limitations, little or no flexibility remains in how individuals can be arranged across the landscape, with all solutions converging toward contiguous Gaussian-like spatial distributions [subject to saturation capacity limits and preferences for individual habitat cells (Figs 3, 5, 6c,d)]. In our model, reaction–diffusion processes become strongly limiting when: (i) reproduction and dispersal rates approach an extinction threshold (regardless of landscape-level limiting factors); and when (ii) site occupancy preferences are strong enough to cause reproduction and dispersal to become limiting, even though a small fraction of the population may actually use those sites.

Conventional wisdom might lead one to suspect that highly fragmented populations are subject to greater extinction risks because the organisms are only loosely ‘connected’ in the habitat complex (Gilpin 1987). While this may often be the case, our results indicate that some fragmented populations could instead be in a very viable state. In the presence of macro-scale limiting factors, a fragmented population arrangement may be one of many alternative patterns that bear no implication to extinction risk. Similarly, when passively diffusing populations are highly clustered, population persistence may still be of concern, depending upon how near the reaction–diffusion processes are to extinction threshold conditions.

An unanticipated result of our experiments is that equilibrium population clustering occurs when strong habitat preferences are introduced, even though few members of the clusters may actually occupy the preferred cells. Although we expected some local clustering within and around preferred cells, we did not expect to observe strong population attraction around preferred sites with passive diffusion. Population contiguity indices for the habitat preference experiments were among the highest that we observed (Table 1). We anticipated that such results would require biased diffusion models (e.g. Allen 1983) that include gregarious density-dependent movement or have a strong species association with an environmental variable that clusters spatially (Westman 1980). Instead, we found that highly clustered populations can result from very localized

site preference, as has been observed with species exhibiting strong site tenacity (Henschel & Lubin 1997). What appears to be gregarious behaviour or a strong association between populations and some environmental gradient may, in some cases, stem from random diffusion processes in the presence of multi-scale limiting factors and local site preferences.

Our results offer a potential explanation for why species–habitat association studies have been characterized by high variability (see Collins 1983). When occupancy patterns from similar sites are compared, variable results could arise from the existence of alternative equilibrium population arrangements even when those sites are subject to identical sets of limiting habitat factors. Furthermore, if population clusters occur across a landscape in response to local site preferences, then estimates of association between populations and environmental factors could be misleading or remain undetected if conditions at the local site are not representative of conditions measured throughout the cluster (Orians & Wittenberger 1991).

These experiments suggest that interpreting the spatial arrangement of populations may be particularly difficult in the absence of fairly detailed information on population growth rates, dispersal, and the factors (including their scale of influence) limiting population size. However, our observations are tied to a specific model formulation, its attendant simplifications, and the limited parameter set explored in our numerical analyses; for example, we have examined the spatial pattern of populations within a closed system. Our landscape was treated as a spatially autonomous patch with no immigration and with an absorbing boundary such that individuals dispersing beyond the patch were assumed to perish. While this may be appropriate for modeling isolated systems, we would expect patterns within systems open to immigration to exhibit smaller habitat size thresholds (see Pagel & Payne 1996), resulting in flexibility for equilibrium population arrangements over a broader range of reproduction and dispersal parameter values. Likewise, we have only examined a single-patch system, but critical habitat size and arrangement thresholds have also been shown to exist for multi-patch reaction–diffusion systems (Bevers & Flather 1999). In such systems, we would expect any increases in disperser survivorship resulting from biased diffusion or a somewhat hospitable inter-patch matrix also to extend the range of parameter values over which many equally ‘good’ population arrangements could be observed.

Movements underlying the ecological process represented by the landscape-level constraint (eqn 3) are also an important consideration in the applicability of our model. At the finer scale, organism

movements are modelled by a reaction–diffusion process. When the landscape-level constraint represents activities by other system components such as predators or disturbance agents, our formulation seems reasonable. On the other hand, when the landscape-level constraint represents processes involving movements by the same organisms as those modelled at the finer scale, as in a forage constraint, our formulation may only apply in fairly restricted cases. It may be appropriate for species that have a strong fidelity to natal breeding sites and that obtain much of their food supply from the surrounding landscape, but we do not expect this formulation to be applicable to territorial species in general. Energetic costs (Covich 1976; Orians & Pearson 1979) or sensitivity to intraspecific interference (Dolman & Sutherland 1997) associated with foraging may limit food acquisition to areas that are in proximity to breeding sites. The effects of restricting foraging movements to account for energetic costs have been examined by Bevers & Hof (1999) using a reaction–diffusion model similar to ours. Their formulation resulted in smaller breeding clusters that were more dispersed throughout the landscape than we observed in our results. Although the species distributional patterns observed with a foraging movement limitation differed from those we report here, they do not contradict our findings. Rather, they tend to emphasize our conclusion that fragmented populations may be very viable as an outcome of multi-scale limitations.

While we have anticipated a number of qualitative effects of relaxing the simple biological assumptions used in this study, further quantitative experiments to test these expectations are warranted. Given the questions raised here concerning the detection of environmental associations with population patterns, broader multi-scale research on these topics should also be useful.

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Appendix

CONTIGUITY MEASURES

The degree of clustering in population distributions is estimated by first converting each solution to a binary map (if $v_i > 0$, then $v_i = 1$, otherwise $v_i = 0$) reflecting the pattern of cell occupancy across the landscape. Clustering in binary maps can be tested using join-count statistics (Dacey 1968; Cliff & Ord 1981) where two cells sharing a boundary within a lattice are said to be linked by a join. Clustering in

the pattern of cell occupancy is determined by counting the number of joins among cells that are first-order neighbours (cells that share a common edge or vertex) and comparing it to the number expected under the null hypothesis of no spatial autocorrelation among the cells. Following the procedures in Gatrell (1977, p. 36), we estimate z_{mn} as a measure of the deviation between observed join-counts and the count expected under the null hypothesis of spatial independence between map elements m and n , where m and n take on values of 0 for the unoccupied map element and 1 for the occupied map element in our case. A spatial clustering statistic is estimated as:

$$z_{mn} = (O_{mn} - E_{mn})/\sigma_{mn}$$

where O_{mn} is the observed join-count between map elements m and n , E_{mn} is the expected count under the null hypothesis of no spatial dependence, σ_{mn} is the standard deviation, and z_{mn} is interpreted as a standard normal deviate. Formulae for E_{mn} and σ_{mn} under sampling without replacement are given by Cliff & Ord (1981, p. 20). We are interested in the pattern among occupied cells. Therefore, $z_{11} > 0$ indicates a tendency for occupied cells to be clustered and $z_{11} < 0$ indicates hyperdispersion or avoidance among occupied cells.

Concentration of population abundance is estimated as:

$$K = \left(\sum_{i=1}^N v_i/b_i \right) / \sum_{i=1}^N \delta_i$$

where $\delta_i = 1$ when $v_i > 0$. Therefore, K is simply the mean standardized abundance observed in occupied cells. Because we have standardized abundance as a simple index reflecting the proportion of occupied cellular carrying capacity, our statistic for abundance approaches 1.0 under maximum concentration.

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