

## Habitat availability causes the species abundance–distribution relationship

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The objective of this study was to examine the effect of different amounts of available habitat on the relationship between the distribution and abundance of species using a spatially explicit, stochastic, individual-based simulation model. We define abundance as the mean abundance of a species in occupied breeding habitat sites and distribution as the proportion of breeding habitat sites that are occupied by that species. We hypothesized that on a patchy landscape, more available breeding habitat will result in both higher abundance and wider distribution because of an increased number of successful dispersers. Therefore, a positive relationship between distribution and abundance is expected for a group of species in a landscape if individual species have differences in habitat use and therefore different amounts of habitat are available to them on the same landscape. In the simulation experiment the amount of breeding habitat was varied to examine the effects on abundance and distribution. We found a positive correlation between (1) abundance and the number of breeding habitat cells on the simulation landscape (2) distribution and the number of breeding habitat cells on the landscape and, (3) abundance and distribution. These results suggest that differences in amount of available habitat could account for a positive relationship between abundance and distribution.

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A positive relationship between local abundance of individuals and their distribution has been demonstrated in numerous groups of taxa and at many different scales (see Gaston and Lawton 1990 for review). This relationship has been attributed to artifacts of sampling (Wright 1991), patterns of resource use (Brown 1984), and differences among species in movement patterns within metapopulations (Gyllenberg and Hanski 1992); and has been reviewed recently in the context of these three hypotheses (Hanski et al. 1993, Gaston 1994).

The purpose of this study was to examine the effect of different amounts of available habitat on the relationship between abundance and distribution using a spatially explicit simulation model.

Distribution has been defined as both the range of a species (Gaston 1990) and as the amount (or percent) of area within a region that a species uses (Hanski 1982). In this paper we use the latter definition and we measure the amount of area used by calculating the proportion of sites occupied, where a site is defined as potential breeding habitat. We define abundance as the mean abundance in occupied sites.

The sampling hypothesis as argued by Wright (1991), suggested that if individuals of a species were distributed randomly (Poisson distribution) at sites, and some species were more abundant than others, then the expected relationship between distribution and abundance would be positive, and therefore no explanation would be necessary. However, he also acknowledges

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that in most species, individuals are not distributed randomly, but as a negative binomial, which also generates the positive relationship. The definition of the negative binomial distribution requires a clumping parameter and is therefore not suitable as a null model. Since there is no a priori null distribution for individuals of a species, and one can imagine a set of distributions for a group of species in which the relationship between distribution and abundance is not positive, it seems appropriate to examine other possible hypotheses for the relationship.

Brown's (1984) hypothesis suggests that the relationship exists because of differences among species in their abilities to use resources. Species that are able to use many different kinds of resources (generalists) would have a greater distribution than specialists because their resources would be more likely to be found over a greater range or in more places. Therefore, using either range size or amount of area used, this hypothesis predicts that generalists should have wider distributions than specialists. In addition, Brown (1984) argued that generalists would be more abundant locally because they would have more resources available to them at any one place. The empirical evidence for Brown's hypothesis is equivocal. Seagle and McCracken (1986) found no correlation between abundance and niche breadth for 4 separate taxa including small mammals, slugs, salamanders, and wintering bird assemblages. Other negative evidence exists for plants (Adams and Anderson 1982) and birds (Ricklefs 1972). There are also studies that support the hypothesis for insects (Mullenberg et al. 1977, Hanski and Koskela 1978) and plants (Parrish and Bazzaz 1976, Johnson 1977). Intuitively, the first half of Brown's argument is easier to accept than the second. That species that can use more habitat types will occupy more area or be found in more places seems plausible, the exception being species that specialize on a single very common habitat type. At a local site however, more resources are not necessarily available to a generalist than a specialist especially if generalists use resources less efficiently than specialists.

A third hypothesis, the metapopulation hypothesis (Hanski et al. 1993), also predicts a positive relationship between the local abundance at occupied sites and the fraction of occupied sites (distribution), given an assemblage of species with variation in one or more of (1) dispersal rate in relation to intrinsic growth rate, (2) probability that a disperser finds a patch before dying or (3) extinction rate in relation to rate of successful colonization. These predictions are based on a structured metapopulation model (Hanski 1991) in which local population size is affected by dispersal between patches as well as by dynamics within patches. The underlying mechanism of the metapopulation hypothesis is variation in the rate of successful dispersal.

Landscape structure affects dispersal success (Dunning et al. 1992, Taylor et al. 1993, Fahrig and Merriam 1994), and amount of habitat on a landscape is a fundamental component of landscape structure. Species within the assemblages that have been used to demonstrate the empirical abundance-distribution relationship are usually taxonomically related but show substantial differences in the kinds of habitat they use. Therefore any given landscape will offer a different amount of habitat to each species within a group of such organisms. We hypothesized that these differences in habitat availability will have a strong effect on the success rate of dispersers. This will lead to a positive relationship between distribution and abundance through the mechanism proposed by Gyllenberg and Hanski (1992).

If the abundance-distribution relationship relies on differences in amount of available habitat then, on average, generalists will be more widely distributed and more abundant than specialists because they will, on average, have more habitat available to them. Whereas Brown's (1984) hypothesis argued that species that could use more types of resources would have a wider distribution, we have generalized this to suggest that species that have more resources available to them will have a wider distribution. Thus, specialists that specialize on a common habitat type should have high abundance and wide distribution.

We used a spatially explicit, stochastic and individual-based model to examine the influence of habitat amount on distribution and abundance. The amount of breeding habitat on the simulation grid was varied and related to the abundance and distribution of individuals on the grid. The simulations demonstrate that availability of habitat on a landscape can generate a positive relationship between distribution as measured by the proportion of occupied sites and the mean abundance in occupied sites. This relationship arises in the absence of variation in resource specialization or dispersal ability.

## Methods

### Model overview

In the simulation model, space is represented by a two-dimensional rectangular landscape of 900 "cells" (30 by 30). There are two kinds of landscape cells: breeding habitat and non-breeding habitat. Individuals may die, reproduce, and/or move within each time step; the order of these events is randomized for each individual in each time step. Parameters in the model can be divided into three general categories: (1) parameters determining the spatial structure of the landscape, (2) demographic parameters determining reproduction and mortality, and (3) movement parameters (see Table 1 for a list of all parameters and their values).

## Landscape

The parameter of interest for this examination is COVER, the proportion of landscape in breeding habitat. COVER was varied randomly between 0 and 1 between simulation runs. The spatial pattern of the breeding habitat on the landscape is specified by a clumping parameter which determines the degree of spatial contagion in the distribution of breeding habitat cells. The algorithm for setting up the spatial pattern of breeding habitat on the landscape is essentially the same as correlated or interacting percolation models (Anderson and Family 1988, reviewed by Plotnik and Gardner 1993). The clumping parameter was set at 0.05 for all simulation runs, which results in moderate clumping. The pattern of breeding habitat is fixed for each simulation run.

## Demographics and movement

Reproduction occurs only in breeding habitat and is determined by the probability of reproduction per time step per individual and the number of offspring per reproduction event. The probability of reproduction is density-independent. However the within cell population is not permitted to exceed the maximum cell occupancy. The probability of mortality is specified separately for breeding and non-breeding habitat (see Table 1 for values).

Movement direction of individuals is random. Movement distance is also random, but is limited to a maximum distance. From the point of view of moving individuals, the landscape is "wrapped"; an individual

that crosses the edge of the landscape continues in the same direction on the opposite edge (Haefner et al. 1991).

## Simulations

The proportion of the landscape in breeding habitat (COVER) was selected randomly for each simulation run. We conducted 100 simulation runs. Each simulation began with 500 individuals distributed randomly over the landscape and was conducted for 500 time steps. The output variables were the number of individuals in breeding habitat cells and the number of occupied breeding habitat cells at each time step. The two response variables were (1) mean abundance of occupied breeding habitat cells (abundance) and (2) the proportion of breeding habitat cells that were occupied (distribution).

The combination of a large maximum movement distance (10), a high probability of movement of individuals in non-breeding habitat (1), and a high probability of mortality in non-breeding habitat (0.5) ensured that most individuals on the landscape were found in breeding habitat.

## Results

We examined the relationship between the amount of breeding habitat on the simulation landscape (COVER) and both the mean abundance in occupied cells and the distribution (proportion of breeding cells that are occupied). Populations in landscapes with less than 5% COVER were extinct within 500 time steps ( $n = 3$ ). In general, landscapes with less breeding habitat took more time steps to stabilize but there were no visible trends in either mean abundance or distribution after approximately 250 time steps (see Figs 1 and 2 for examples of simulation runs with 86% COVER and 24% COVER). After populations had stabilized there was a positive relationship between COVER and the mean abundance in occupied habitat (Fig. 3; Spearman Rank Correlation;  $\rho = 0.81$ ,  $p = 0.0001$ ,  $n = 97$ , calculated at time step 500). There was also a positive relationship between the amount of breeding habitat and the distribution after populations were stabilized (Fig. 4; Spearman Rank Correlation,  $\rho = 0.95$ ,  $p = 0.0001$ ,  $n = 100$ ). Mean abundance and distribution are therefore strongly correlated (Fig. 5; Spearman Rank Correlation,  $\rho = 0.86$ ,  $p = 0.0001$ ,  $n = 97$ ). In addition, mean abundance and distribution are not correlated when COVER is controlled for using partial correlation (Partial Spearman Rank Correlation,  $\rho = -0.01$ ,  $p = 0.92$ ,  $n = 97$ ), indicating that the correlation between abundance and distribution is due to the effect of COVER on each.

Table 1. Parameter values used in the simulation experiment.

1. Spatial structure of the landscape	
Landscape size (no. of cells)	900
Proportion of grid in breeding habitat (COVER)	Varied (0-1)
Breeding habitat clumping parameter	0.05
2. Demographic parameters determining reproduction and mortality	
Starting number of individuals	500
Maximum cell occupancy	10
Reproduction probability	0.5
Offspring per reproduction	1
Mortality probability in breeding habitat	0.3
Mortality probability in non-breeding habitat	0.5
3. Movement parameters	
Maximum movement distance	10
Movement probability in breeding habitat	0.05
Movement probability in non-breeding habitat	1.0

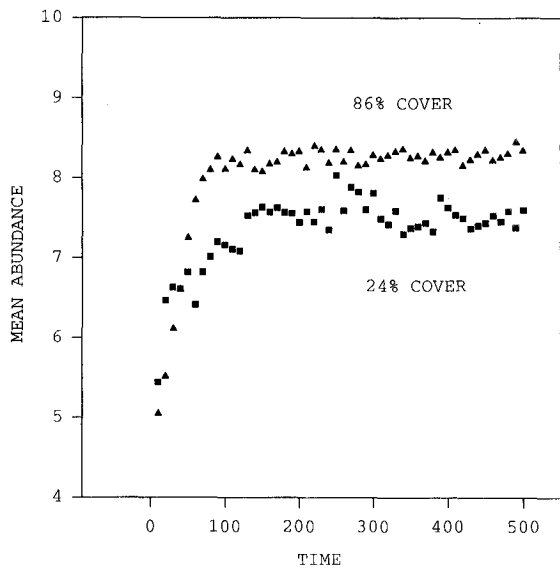


Fig. 1. Mean abundance per occupied breeding habitat cell plotted against time at intervals of 10 time steps for two sample landscapes with 86% COVER and 24% COVER.

The simulation results also indicate that there is more variation in the mean abundance at lower levels of distribution (Fig. 5). All points below a distribution of 0.7 had less than 15% breeding habitat (COVER), and a wide range of mean abundances (5.2 to 8.7; Fig. 5).

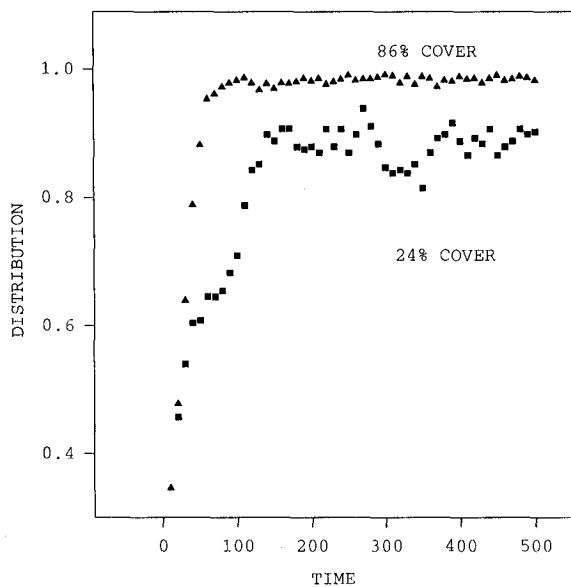


Fig. 2. Distribution plotted against time at intervals of 10 time steps for two sample landscapes with 86% COVER and 24% COVER.

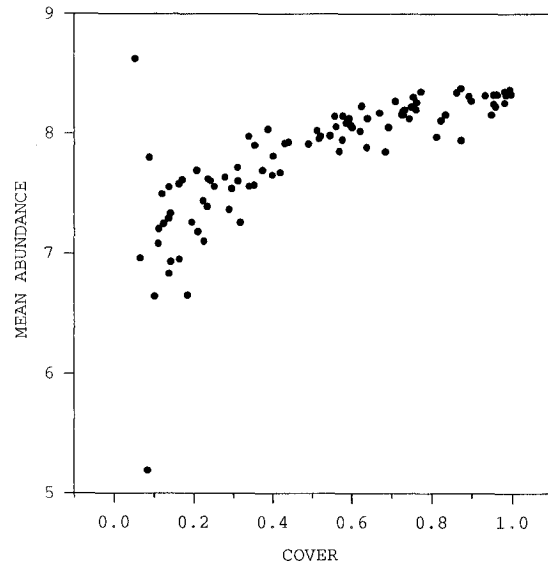


Fig. 3. Mean abundance per occupied breeding cell plotted against COVER (proportion of the total landscape area in breeding habitat) for 100 simulation runs. Data are from the 500th time step for each run. Spearman rank correlation;  $\rho = 0.81$ ,  $p = 0.0001$ ,  $n = 97$ .

## Discussion

The results from our simulations suggest that differences in amount of available breeding habitat for species, all other things being equal, can account for a positive relationship between distribution and abun-

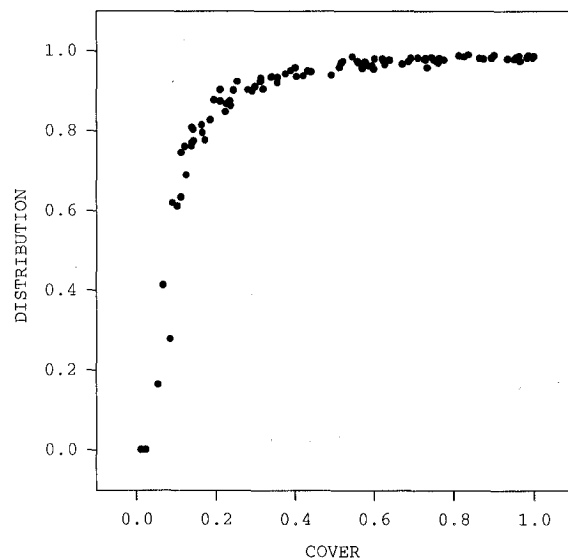


Fig. 4. Distribution (measured as the proportion of breeding habitat cells that are occupied) plotted against COVER (proportion of the total landscape area in breeding habitat) for 100 simulation runs. Data are from the 500th time step for each run. Spearman rank correlation;  $\rho = 0.95$ ,  $p = 0.0001$ ,  $n = 100$ .

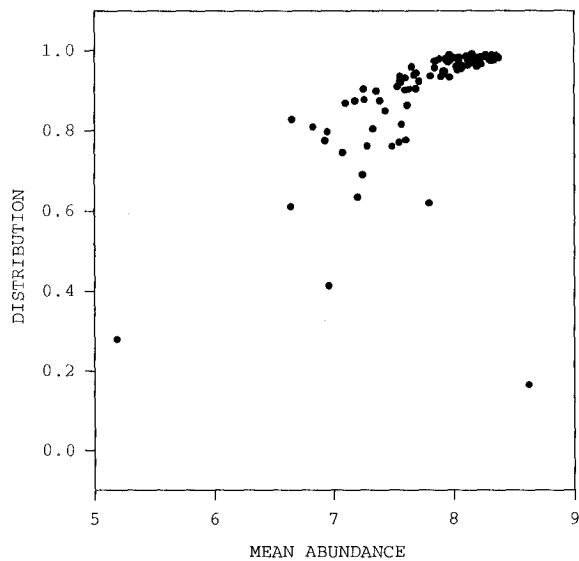


Fig. 5. Distribution plotted against mean abundance at the 500th time step, for 100 simulation runs. Spearman rank correlation;  $\rho = 0.86$ ,  $p = 0.0001$ ,  $n = 97$ .

dance of species. Landscapes with more breeding habitat reached a higher mean abundance level and a greater distribution and did so more quickly than landscapes with less breeding habitat, resulting in a positive relationship between abundance and distribution.

On a single landscape, each species of an assemblage will perceive the habitat composition differently to a lesser or greater degree, depending on habitat preferences, and therefore different amounts of habitat will be available to each species. Most landscapes consist of many types of habitat in different amounts. Those species that use a higher percentage of the landscape by using more common habitat types or more habitat types (generalists), are expected to be both more abundant and more widely distributed.

Success rate of dispersers, as defined by the probability of finding a patch before dying, is the mechanism through which amount of available habitat influences abundance and distribution. Dispersal is more likely to be successful when there is more habitat available to disperse to. Several empirical studies indicate that immigration can increase the size of small populations (Connor et al. 1983, Rey and Strong 1983, Fahrig and Merriam 1985). Askins et al. (1987) indicate that for forest-interior birds, density is higher in forest patches that occur in regions of abundant forest and they suggest that dispersal from other forests may be contributing to maintaining the local population. This result supports the suggestion of Ambuel and Temple (1983) that forest-interior bird populations are regional in that population levels are dependent on the regional forest content.

The metapopulation hypothesis (Hanski et al. 1993) suggests that in many natural assemblages, species differ

from one another in several respects. Variation in one or more of (1) dispersal rate in relation to intrinsic growth rate, (2) probability that a disperser finds a patch before dying or (3) extinction rate in relation to rate of successful colonization results in a positive relationship between distribution and abundance (Gyllenberg and Hanski 1992). The metapopulation hypothesis was formulated using modelling studies in which the amount of available habitat was fixed and the population parameters were varied. In contrast, we varied habitat availability while holding population parameters constant. We are proposing that the factor controlling the success of dispersers is likely to be the amount of available habitat. This is not explicitly dealt with in the formulation or discussion of the metapopulation hypothesis (Gyllenberg and Hanski 1992). Differences in disperser success can account for the abundance-distribution relationship as argued by Hanski et al. (1993). However we hypothesize that differences in disperser success are consistently expected both between and within species because of differences in habitat availability.

Many empirical studies of the relationship between distribution and abundance are conducted on assemblages of taxonomically related species, but these species do not necessarily have the same habitat usages. Several studies, for example, rely on wintering bird data for a large variety of species in North America (Bock and Ricklefs 1983, Bock 1984). We argue that under conditions where the abundance-distribution relationship exists and species are likely to have different habitat usages, differences in habitat availability is the simplest and most likely cause for the relationship. The relationship need not rely on differences in demographic characteristics between species.

If the abundance-distribution relationship results from variation in habitat availability then we predict a positive relationship between abundance and distribution for single species, where distribution and abundance are measured in a variety of regions that vary in habitat composition. In this case, differences in niche breadth among populations within the species are not likely to account for the relationship. Therefore the resource-use hypothesis (Brown 1984) would not apply, and species differences in parameters such as dispersal rate or dispersal distance would not be relevant. Positive intra-specific relationships between mean abundance and distribution have been examined at very fine scales to develop efficient sampling schemes for pest insects (Wilson and Room 1983, Ward et al. 1986, Hergstrom and Niall 1990, Yamamura 1990). There is some work at coarser scales (Bart and Klosiewski 1989, Robbins et al. 1989), which assesses the usefulness of presence-absence measures to detect changes in bird population density over time, and reveals a positive relationship between mean abundance and distribution. These studies lend support to the idea that the positive distribution-abundance relationship is not dependent

on interspecific differences. However in most of the above mentioned studies mean abundance is calculated from all sites not just occupied sites, which confounds the result.

Our model has some simplifying assumptions including density independent reproduction and dispersal. The rate of mortality is somewhat density dependent in that there is a ceiling on the number of individuals within each cell. In any case, we do not anticipate that density dependent reproduction or mortality would qualitatively influence the expected relationship between distribution and abundance. The overall cell densities are expected to be lower but the effects of disperser success on both abundance and distribution are the same. Density dependent dispersal, with an increased rate of dispersal with increasing cell density, will reduce the density of the highest cells relative to lower density cells but overall there will be more dispersal and therefore likely more successful dispersal when average abundance is higher. Therefore the form of the relationship is not expected to change.

The relationship between abundance and distribution appears to hold less well at low levels of breeding habitat than when breeding habitat is abundant (Fig. 5). Some cells can reach high abundance in the absence of successful dispersal due to stochastic reproduction and mortality. At low levels of breeding habitat these cells will have a large impact on the mean abundance. However, whether a cell is occupied or not depends almost entirely on the amount of successful dispersal which will be low at low levels of breeding habitat. Therefore we expect and find more variation in mean abundance than in distribution at low levels of breeding habitat (see Figs 3 and 4).

The relationship between regional habitat availability and both distribution and local abundance is significant to problems of conservation. For example, the relationship between population size and the amount of available habitat is not linear if the mean local abundance decreases with decreasing amount of habitat regionally. Therefore, it is necessary to understand the form and magnitude of this relationship to make estimates of the impact of habitat removal on population size and viability.

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