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The importance of the relationship between population density and habitat area

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The relationship between population density and habitat size, the density-area relationship, has received considerable, but often sporadic and unfocused attention (Root 1973, Risch 1981, Kareiva 1983, Bach 1988, Matter 1997). Recent reviews of the topic have revealed that there is a great deal of variability in the relationship with species showing patterns of increasing, decreasing, and constant density with habitat size (Bowers and Matter 1997, Bender et al. 1998, Connor et al. 2000). Despite this considerable variability, the overall trend across species appears to be increasing density with habitat size, especially for insects and birds (Bender et al. 1998, Connor et al. 2000; but see Gaston et al. 1999). Mammals show fairly constant densities with habitat area with about as many positive as negative density-area relationships (Bowers and Matter 1997, Connor et al. 2000).

A variety of different mechanisms have been offered to account for density-area relationships. Root (1973) explained the positive density-area relationship seen for herbivorous insects in the 'resource concentration hypothesis'. He proposed that density would increase with area via dispersal if emigration rates were greater for smaller, and immigration rates were greater for larger patches (Root 1973). Subsequently, predatory rates (Risch 1981), habitat quality (Hanski 1994, Matter 1997), and social interactions (Bowers and Matter 1997, Bowers and Dooley 1999) that vary with patch size have been proposed to account for both positive and negative density-area relationships. Bowers and Matter (1997) proposed that habitat selection at small spatial scales may produce negative density-area relationships while positive relationships may arise at larger scales through colonization-extinction dynamics. Density-area

relationships may also arise from methodological problems such as the mis-estimation of patch size for edge and interior species (Bender et al. 1998) or increasing amounts of non-habitat with census area (Smallwood and Schonewald 1996, Gaston et al. 1999). Gaston et al. (1999) detail many of the problems that can occur when estimating density-area relationships; however, many of the statistical problems discussed can be avoided through the use of alternative methods. Gaston et al. (1999) point out that for log density-log area plots the minimum allowable value is $1/\text{area}$, which may produce a non-zero expected slope as well as heteroscedasticity. These statistical difficulties can be overcome by using an area-sensitive Poisson model (Feller 1968, Connor et al. 1997, Matter 1997). Here the expected abundance of organisms at a site is simply the mean density across all sites multiplied by site area raised to a power. This model can be fit with and without the exponent using generalized linear models to determine if *density* varies with area. The model has the advantage of having the appropriate variance structure and allows for the inclusion of inhabitable sites with zero density (Matter 1997).

Despite research describing patterns of density with habitat area and attempting to attribute mechanisms responsible for it, researchers have yet to appreciate the importance of density-area relationships in a wider context. Similar to patterns of aggregation, density-area patterns influence a variety of ecological processes. Here, I illustrate how the density-area relationship of individual species is of fundamental importance for spatial population and community ecology and is pertinent to conservation issues.

Metapopulation dynamics

Density-area relationships play a critical role in metapopulation dynamics. Despite recognizing that density may vary with area (Hanski 1994), no attempt has ever been made to show how metapopulations of species with different density-area relationships may behave differently in the same patch network. Here, I demonstrate differences in the expected lifetimes and patch occupancy patterns of species with the same metapopulation parameters but differing density-area relationships.

The importance of the density-area relationship for a single species can be shown using the 'incidence function model' (Hanski 1994, Hanski et al. 1996). In this model extinction risk (E) is assumed to be proportional to local population size and is thus related to habitat area (A) via the function:

$$E_i = \frac{e}{A_i^x},$$

where e and x are two constants (Hanski 1994). It should be noted that the parameter x here could be considered to scale the density-area relationship, but Hanski (1994) has interpreted this parameter to be a measure of susceptibility to environmental stochasticity,

which may or may not covary with the density-area relationship. I will keep that assumption here.

Colonization of patches is assumed to depend on their 'connectedness' (the inverse of isolation) via the function:

$$C_i = \frac{S_i^2}{S_i^2 + y^2}$$

where:

$$S_i = \beta \sum_{j=1, j \neq i}^n P_j e^{-\alpha d_{ij}} A_j$$

and S_i is the number of migrants to patch i , d_{ij} is the distance between patch i and j , $P_j = 1$ for occupied and $P_j = 0$ for unoccupied patches, and y , α , and β are three parameters.

To create density-area relationships I used two approaches, both assuming that the number of individuals is related to habitat area. The first was that recommended by Hanski et al. (1996) transforming the area of each patch to its 'effective area' through the use of an exponent:

$$A_{ei} = A_i^b.$$

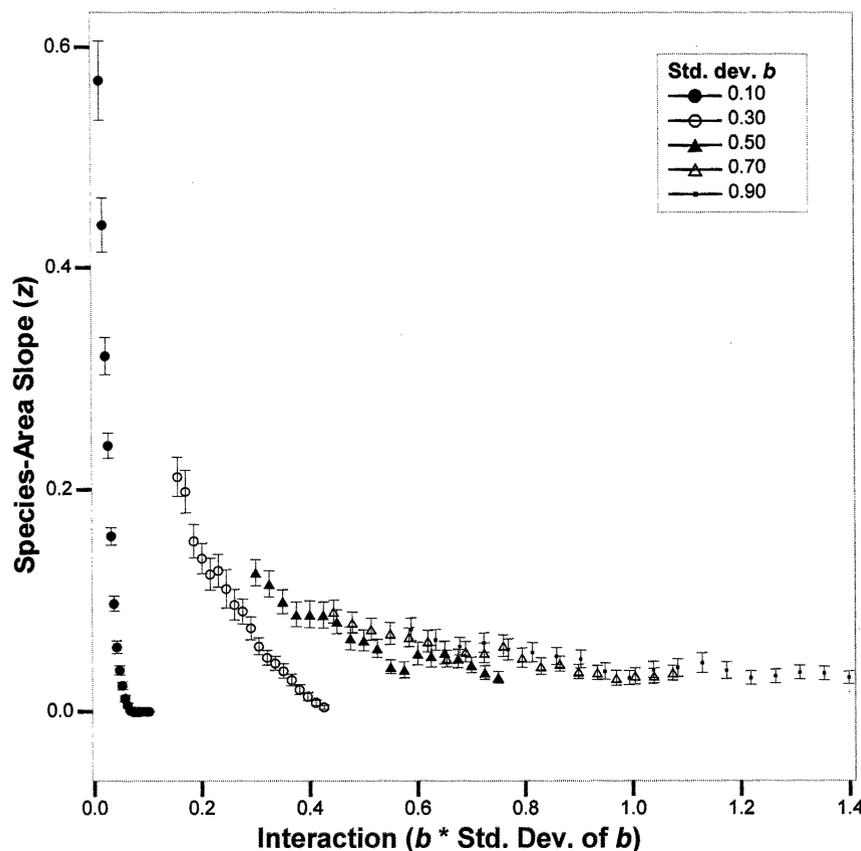
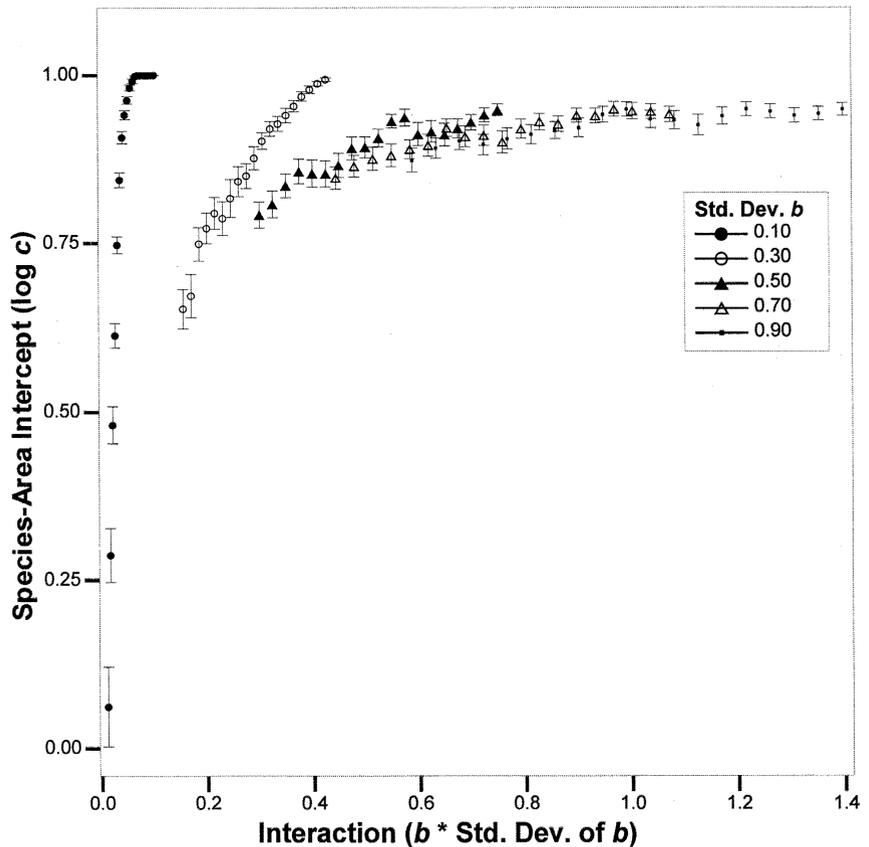


Fig. 1. The species-area slope (z) generated for communities with different mean values of the density-area relationship (b) and different amounts of variation in b . The species-area slope is plotted versus the interaction between the mean and standard deviation of the distribution of density-area relationship. Each group of symbols represents a common standard deviation and points within a symbol type different mean values from $b = 0.6$ to $b = 1.5$. Each point represents the mean and bars the standard error of fifty replicate simulations.

Fig. 2. The species-area intercept ($\log c$) generated for communities with different mean values of the density-area relationship (b) and different amounts of variation in b . The species-area intercept is plotted versus the interaction between the mean and standard deviation of the distribution of density-area relationship. Each group of symbols represents a common standard deviation and points within a symbol type different mean values from $b = 0.6$ to $b = 1.5$. Each point represents the mean and bars the standard error of fifty replicate simulations.



Unfortunately for comparative purposes, this method results in different total areas for different values of b . Thus to keep the pooled patch area constant and simply test for density-area relationship effects, I also used a second method:

$$A_{ei} = \frac{nA_i^b}{\sum A_j^b} \sum A_j$$

For both methods values of $b = 1.0$, 0.8 , and 1.2 were used to create constant, decreasing, and increasing density-area patterns, respectively. I simulated the dynamics of each density-area pattern over 1000 generations using the freeware version of the incidence function model and the accompanying Glanville fritillary (*Melitaea cinxia*) data set provided by A. Moilanen [http://www.helsinki.fi/science/metapop/softa.html]. The model was run using parameters as for the sample data set and the data were unchanged except for their effective areas. Twenty replicate runs were conducted for each level of b for both methods.

The results of this exercise clearly demonstrate the sensitivity of metapopulations to density-area relationships. Under the assumption of constant local population density with area ($b = 1.0$) one of twenty simulations showed extinction of the entire metapopu-

lation with a mean patch occupancy over the 1000 generations of 0.46 ± 0.02 (standard deviation). When density was decreasing with area ($b = 0.8$) metapopulations in all twenty simulations went extinct. When density was increasing with area ($b = 1.2$) no extinctions occurred and the mean patch occupancy was 0.99 ± 0.00 . As noted above, these extreme results are due to different total patch areas for different values of b . When total area was held constant there were still large differences due solely to the density-area relationship. When density was increasing with area and total area was held constant, eight metapopulation extinctions occurred and mean patch occupancy was 0.31 ± 0.14 (0.39 ± 0.02 for simulations without extinction). When density was decreasing with area and total area was constant no extinctions occurred and mean patch occupancy was 0.55 ± 0.01 . The constant density-area relationship ($b = 1.0$) was the same as for the first analysis, showing one metapopulation extinction.

It should be noted that the values of b used in this illustration are not extreme. A value of $b = 0.5$ was used to modify areas for connectedness by Hanski et al. (1996). For extinction, however, they considered the parameter x to be the product of both environmental stochasticity and the scaling of the number of individuals with area (Hanski et al. 1996). I have found that abundance scales with area at a power of 1.6 for the beetle *Tetraopes tetraophthalmus* (Matter 1997).

It is easy to appreciate how density-area relationships will affect both the 'connectedness' and the extinction rates of local populations by changing the relative importance of certain patches or groups of patches within a metapopulation. If the density-area relationship is positive, larger patches have an even greater importance because they contain proportionally more individuals, produce more colonists, and have a lower risk of extinction. Smaller patches have fewer individuals and are subject to higher extinction risk. The converse is true if the density-area relationship is negative. However, whether metapopulations of species with positive, negative, or constant density-area relationships are more prone to metapopulation extinction depends on the particular landscape configuration. Thus, habitat change or fragmentation may have different effects for metapopulations with different density-area relationships and also within different landscapes.

Community-level patterns

The density-area relationship is intimately related to the species-area relationship. That the form of the species-area relationship depends on the density-area relationships of the component species can be shown theoretically. For the sake of illustration, we can as-

sume that species abundance follows a lognormal distribution. Preston (1962) showed that under these conditions the following relationship holds:

$$\log S = 0.263 \log(J/m) + 0.317,$$

where S is the number of species, J is the number of organisms on a given island, and m is the number of organisms of the rarest species. In deriving the expected slope of the species-area relationship Preston next defined:

$$J = \rho A,$$

where ρ is 'organismal' density and A is island area. We can relax the assumption of a constant density-area relationship by modifying this equation as such:

$$J = \rho A^\beta,$$

where β describes the scaling of abundance with island area. Substituting this into the first equation, back-transforming, and assuming $c = 2.07(\rho/m)^{0.263}$ produces:

$$S = cA^{0.263\beta},$$

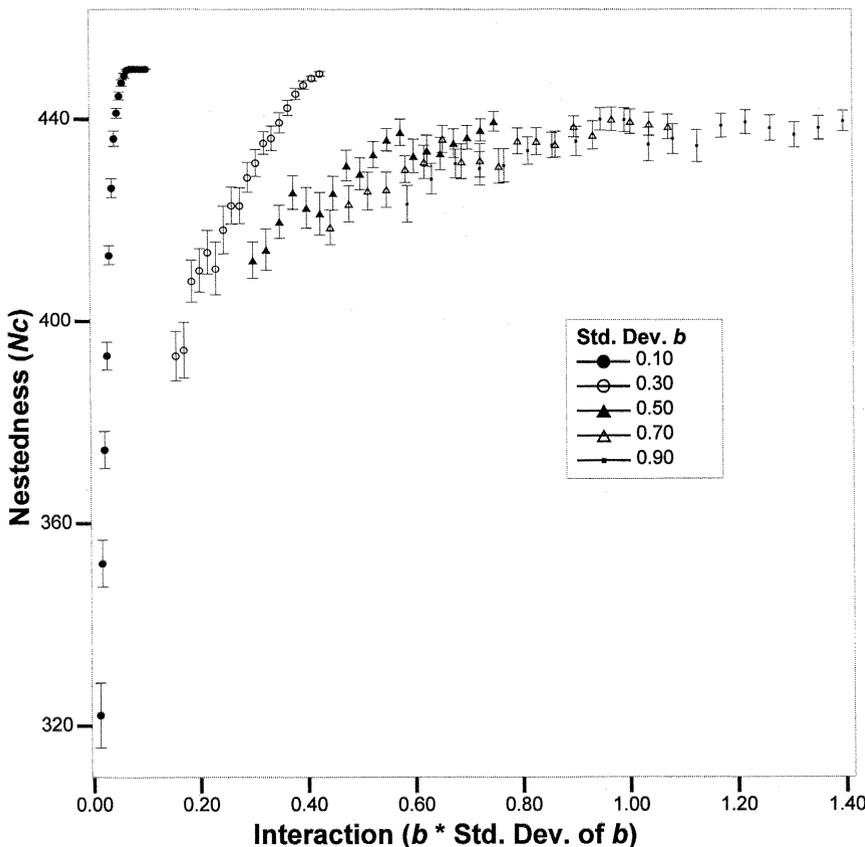
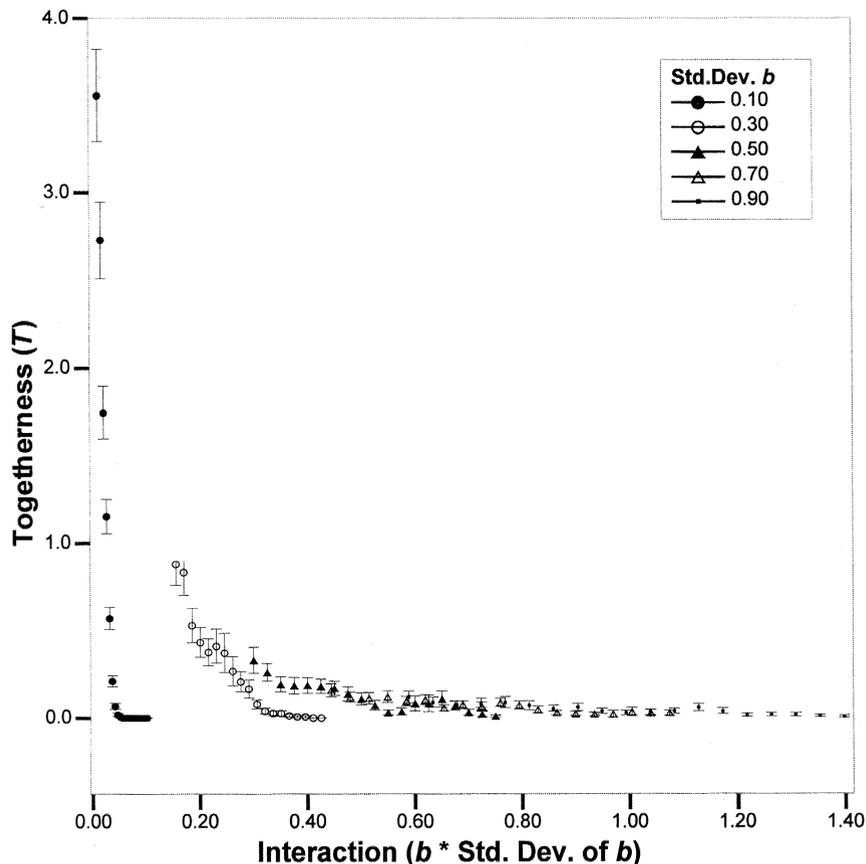


Fig. 3. The nestedness statistic (N_c) generated for communities with different mean values of the density-area relationship (b) and different amounts of variation in b . Nestedness is plotted versus the interaction between the mean and standard deviation of the distribution of density-area relationship. Each group of symbols represents a common standard deviation and points within a symbol type different mean values from $b = 0.6$ to $b = 1.5$. Each point represents the mean and bars the standard error of fifty replicate simulations.

Fig. 4. The community aggregation statistic (T) generated for communities with different mean values of the density-area relationship (b) and different amounts of variation in b . Togetherness is plotted versus the interaction between the mean and standard deviation of the distribution of density-area relationship. Each group of symbols represents a common standard deviation and points within a symbol type different mean values from $b = 0.6$ to $b = 1.5$. Each point represents the mean and bars the standard error of fifty replicate simulations.



which is equivalent to the species-area power function equation (Connor and McCoy 1979) with the expected slope modified by the relationship between density and area. It should be pointed out that in this case β (and ρ) is a community-wide metric, 'averaging' the density-area relationships of species in the assemblage. However, there is no reason to assume that the density-area relationships of all species in an assemblage should be similar (Bowers and Matter 1997, Connor et al. 2000).

The effect of species with different density-area relationships on community patterns is most easily shown by simulation. For this example consider a set of ten islands, ranging in size from 10 to 55 incrementing by five, and a set of ten species each having a different density from 0.06 to 0.15 incrementing by 0.01. The number of individuals of species i on island j is:

$$N_{ij} = \rho_i A_j^{b_i},$$

where ρ_i is the density of species i , A_j is the area of island j , and b_i is a parameter that describes the relationship between density and area for species i . For values of b greater than 1.0, density is increasing with area, and for values less than 1.0, density is decreasing with area. To create different 'communities' I assigned a random value of b from a normal distribution with

mean values from 0.60 to 1.50 incrementing by 0.05 and standard deviations from 0.1 to 0.9 incrementing by 0.2. The only constraints on the communities were that a species had to occur on at least one site, all sites had at least one species, and that fractional individuals were disregarded.

For these sample data sets, I calculated several common community statistics. The first were slope and intercept, z and $\log c$, from the species-area curve, which were calculated via linear regression of log-species versus log-area. Secondly, I examined the 'nestedness' of the community. Nestedness refers to the degree to which the makeup of each progressively less species rich site is a proper subset of richer sites (Wright and Reeves 1992). This statistic has been used to imply the 'orderly' extinction or colonization of sites (McDonald and Brown 1992). To examine nestedness I calculated the ' N_c ' statistic of Wright and Reeves (1992) which is comparable for matrices of equal size. Finally, I examined the aggregation or 'togetherness' (T) of the communities, which describes the degree of aggregation in the community matrix (Stone and Roberts 1992). Fifty replicate communities were created for each factorial combination of mean and standard deviation of b .

The communities were quite different and exhibited consistent trends with both the mean and variance in

the density-area relationships. The slope and intercept of the log-species log-area curve showed a relationship that becomes shallower (smaller slope and greater intercept) with increasingly positive density-area relationships and with greater variation in the density-area relationship (Figs 1, 2). The nestedness (N_c) of the communities tended to increase, while the aggregation (T) decreased with both increasingly positive density-area relationships and increasing variance in the density-area relationship (Figs 3, 4). The purpose here is not to detail differences in community patterns, but to illustrate that these patterns differ because of the density-area relationship. In general, the density-area relationship affects the rate at which sites become occupied, thus affecting the observed community patterns. This rate will also depend on the distribution of densities as well as island sizes. Not incorporating density-area relationships of species in community studies can lead to misinterpretation of statistics and the processes implied by them.

Conservation

Finally, the density-area relationship has a bearing on conservation issues, aside from those associated with community ecology and metapopulation dynamics (Wahlberg et al. 1996). In particular, the density-area relationship speaks to the single-large or several-small (SLOSS) debate. This debate centres on whether one large reserve or several smaller reserves adding to equal size will preserve more species or individuals of a particular species (Simberloff 1988). If the density of a particular species increases with area, one large reserve will contain more individuals than any number of smaller reserves summing to the same area, assuming that 'areas' are equal. The converse is obviously true for situations where density decreases with area. To reach conclusions concerning the number of species preserved it is only necessary to examine the density-area relationship of each species (within their particular habitat type), barring species or site non-independence.

Several important caveats need to be made concerning applying density-area relationships to conservation issues. First, and perhaps foremost, is that density is not always an indication of habitat quality (Van Horne 1983). An example of this is where dominant individuals maintain territories on high quality habitats, and non-territorial sub-dominants are relegated to lower quality habitats producing a negative density-area relationship. Such a mechanism has been proposed to account for the negative density-area relationship seen for the meadow vole, *Microtus pennsylvanicus* (Bowers and Dooley 1999).

A second concern when applying density-area relationships to conservation is variability in the density-

area relationship. Bowers and Matter (1997) and Connor et al. (2000) have shown that density-area relationships were largely consistent for species from which multiple estimates could be derived. However, I have found in my studies of the red milkweed beetle, *Tetraopes tetraophthalmus*, patterns of increasing, decreasing, and constant density with habitat area within the same set of patches over a span of five years (Matter 1997, unpubl). For this system the size and number of habitat patches is quite variable, and I have attributed the variation in the density-area relationship to temporal variation in the landscape. Often species that we wish to preserve are endangered because of habitat loss or degradation. In these situations it may be unclear whether density-area estimates derived in varying habitats will be the same as for the presumably more stable reserves. Thus, a great deal of care must be exercised in both estimating density-area relationships and applying them to a different set of habitat patches.

A final problem is that of scale. Generally, density-area relationships are derived from small or meso-scale systems because it is often difficult to obtain reliable density estimates at large spatial scales. Despite these difficulties, we often want to implement conservation efforts at large scales. Applying density-area relationships derived at one scale to a different scale is akin to extrapolating a regression line. We simply do not have the information needed to make a judgement, unless we assume that the functional form holds for all size patches. There may be good reason to believe that the relationship will differ at different scales. Bowers and Matter (1997) found that at large spatial scales the density-area relationship for mammals was more positive and at smaller scales more negative. We attributed these differences to different mechanisms occurring at different scales. At smaller scales, habitat selection and territoriality may produce negative density-area relationships while a colonization-extinction dynamic at larger spatial scales may produce positive relationships if extinction risk increases with decreasing population size.

Conclusion

The relationship between the density of an organism and the size of the habitat in which it resides is of fundamental importance for spatial population and community ecology. This relationship affects the dynamics of single species and community-level patterns, and may play a role in conservation issues. Researchers need to be aware of and account for these effects when examining spatial population and community issues.

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