Integrating nested spatial scales: implications for the coexistence of competitors on a patchy resource

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Summary

1. Intraspecific aggregation at a single spatial scale can promote the coexistence of competitors. This paper demonstrates how this same mechanism can be applied to the many systems that are patchy at two scales, with patches nested within 'superpatches'.

2. Data are presented from a field study showing that insects living in rotting fruits have aggregated distributions in the fruits under a single tree, and that the mean density and degree of aggregation varies significantly among trees. Observations in this system motivate the following models.

3. A model of competition has been developed between two species which explicitly represents spatial variation at two scales. By integrating the probability distributions for each scale, the marginal distributions of competitors over all patches can be found and used to calculate coexistence criteria. This model assumes global movement of the competitors.

4. Although spatial variation at a single scale may not be sufficient for coexistence, the total variation over all patches can allow coexistence. Variation in mean densities among superpatches and variation in the degree of aggregation among superpatches both promote coexistence, but act in different ways.

5. A second model of competition between two species is described which incorporates the effects of limited movement among superpatches. Limited movement among superpatches generally promotes coexistence, and also leads to correlations among aggregation and the mean densities of competitors.

Key-words: aggregation, coexistence, competition, negative binomial, nested spatial variation.

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Introduction

Many models have shown that multiple species with identical resource use can coexist, if the resource varies spatially or temporally (Atkinson & Shorrocks 1981; Chesson & Warner 1981). Aggregation, or clumping, of competitors can generate spatial variation if the resource occurs in discrete patches. In particular, if a superior competitor is aggregated so that some patches harbour many individuals while others harbour few, then an inferior competitor using the same set of patches may persist indefinitely (Atkinson & Shorrocks 1981; Atkinson & Shorrocks 1984; Ives & May 1985; Ives 1988). As aggregation of the superior competitor increases, the superior competitor suffers more from intraspecific competition, and a higher pro-

portion of patches are left empty for inferior competitors to exploit. Effects of aggregation on coexistence at one spatial scale are well documented; however, many resources are patchy at more than one scale. For a resource that is patchy at two nested scales, 'superpatches' (collections of smaller-scale patches) may exhibit varying degrees of aggregation or densities of competitors, and thus may contribute differentially to coexistence at a regional scale. Previous theory has not addressed how variation in aggregation at different scales may affect the coexistence of competitors. In this paper evidence is first presented from a field system (insect larvae feeding on the fallen fruit of a tropical tree) that the degree of aggregation and density of competitors has a hierarchical spatial structure. Analytical and simulation models are then used to examine how the role of aggregation at nested spatial scales affects the coexistence of competitors.

Although previous models of competitors using patchy and ephemeral resources have considered only

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a single spatial scale of patches, many resources, including fruits, mushrooms and plants in forest gaps can be patchy at more than one scale (e.g. Debouzie, Heizmann & Humblot 1993; Gross, Pregitzer & Burton 1995; van Klinken & Walter 1996; Underwood & Chapman 1996). For instance, for the insect larvae that develop and compete inside rotting fruits, each fruit is a discrete patch, but for the adult insects that determine the distribution of larvae among fruits, resources may appear to be patchy not only at the scale of fruits, but also at the scale of trees. Adults searching for oviposition sites may use one set of cues to find appropriate trees (superpatches rich in oviposition sites), and another set of cues and behaviours to select fruits under each tree. Just as splitting a uniform resource into patches at a single spatial scale can change criteria for the coexistence of competitors, adding a second scale of patches expands the potential for spatial heterogeneity, and thus may alter the range of conditions allowing coexistence.

If a relatively high degree of aggregation of the superior competitor is required for an inferior competitor to persist, and the requisite degree of aggregation occurs in only some superpatches, then these superpatches may play a disproportionate role in determining coexistence. The present study uses a simple model to investigate the degree to which hierarchical variation in the aggregation and density of competitors will facilitate coexistence beyond the effect achieved by aggregation at a single spatial scale. This model implicitly assumes global movement among all patches. To investigate whether limited movement among superpatches changes the importance of hierarchical aggregation for coexistence, a second model is used that relaxes the assumption of global movement, using an approach in which superpatches are viewed as 'islands' with limited migration among them (Kareiva 1990). These models take the general approach of describing spatial variation at each scale with separate probability distributions, and then integrating these distributions to arrive at a description of regional aggregation. Because both of these new models rely on a framework provided by previous work describing aggregation at a single scale, some earlier models and results are first briefly reviewed. A natural system is then described that has spatial variation at two spatial scales.

PREVIOUS MODELS OF AGGREGATION AND THE COEXISTENCE OF COMPETITORS

The aggregation mechanism of coexistence was proposed by Atkinson & Shorrocks (1981, 1984) and Hanski (1981). Shorrocks and coauthors (Shorrocks, Rosewell & Edwards 1990; Shorrocks & Bingley 1994) have since explored several elaborations of their original simulations, by adding priority effects and linking the degree of aggregation and mean density. General conditions for the aggregation mechanism to promote

coexistence were obtained analytically by Ives & May (1985), and Ives (1988). These analyses demonstrated that the probability of an inferior competitor finding a resource patch where the superior competitor is absent depends on the degree of aggregation of the superior competitor. When a superior competitor is more aggregated, coexistence with an inferior competitor becomes possible for even higher intensities of competition.

Unlike the fugitive mechanism of coexistence (Horn & MacArthur 1972) the aggregation mechanism does not require the competitors to differ in their ability to find or colonize patches, nor to be able to detect the presence or absence of individuals already in a patch. In the aggregation mechanism the inferior competitor finds its refuges from the superior competitor by chance, not by ability. For this reason this mechanism has also been called a probability refuge mechanism (Shorrocks 1990). Resource partitioning is not invoked because, in the absence of either competitors or aggregation, all species would have equal performance on all patches, nor are the distributions of species necessarily negatively correlated. The aggregation mechanism of coexistence assumes instead that competing species are independently distributed among patches (but see Rosewell, Shorrocks & Edwards 1990). Ives & May (1985, Ives 1988) investigated the effect of correlated distributions between competitors, and found that resource partitioning can act in concert with aggregation further to promote coexistence.

Neither the simulations nor the analytical models describing the aggregation mechanism explicitly keep track of every individual in every patch. Instead, the distributions of individuals among patches are described by probability distributions. Negative binomial distributions are commonly used to describe the aggregation of individuals among patches because they provide good fits to empirical data (Krebs 1989; Rosewell *et al.* 1990). These statistical descriptions of the distributions of competitors allow calculation of the expected frequency of different combinations of competitors, and thus the frequency of different outcomes of competition. This process ignores details of adult behaviour that are responsible for the spatial patterns, but concentrates on the consequences of aggregation as a life history trait, regardless of its origin.

NESTED SPATIAL PATTERNS IN A NATURAL SYSTEM: METHODS

The theoretical investigations that follow are motivated by the observation that variation among patches exists at two nested spatial scales in a tropical insect community, specifically the insects that feed in the fruits of *Apeiba membranacea* (Tiliaceae), a canopy tree in Central American rainforests. Some of the results supporting this conclusion are described below.

A more complete description and analysis appears elsewhere (Inouye 1988). After they fall and begin to rot, *Apeiba* fruits are rapidly colonized by a wide range of pulp-eating insects, including flies, beetles, moths and predatory arthropods. The four most abundant of these species, on which this study focuses, are a small moth in the subfamily *Tineinae* (Tineidae) and three Diptera, *Chlorops* sp. (Chloropidae), *Taeneaptera* sp. (Micropezidae) and *Richardea* sp. (Richardiidae) (Table 1). These four species were not found in other fruits at La Selva (except for *Taeneaptera* sp., which was once reared from a *Pterocarpus* sp. fruit) Preliminary results of experimental manipulations using the three fly species show that their larvae compete both intra- and interspecifically (Inouye 1998).

Data on the spatial distributions of each species were obtained by collecting 11–36 (mean = 24) fruits from underneath 28 trees at La Selva Biological Research Station, Costa Rica. These fruits were collected from May to July of 1996; patterns similar to those reported below were observed in 1994, 1995 and 1997. After collection, all larvae longer than 1 mm were identified and counted. Because each tree is a discrete patch at a larger spatial scale, i.e. a superpatch, for each species, the mean density of larvae and the degree of aggregation among fruits were calculated separately for each tree. Fruit volume did not vary dramatically (Inouye 1998), so calculations assumed fruits had a constant volume (but see Sevenster 1996).

NESTED SPATIAL PATTERNS IN A NATURAL SYSTEM: RESULTS

Insect larvae were usually significantly aggregated among the fruits under a single *Apeiba* tree (Table 1). Two different measures of aggregation were used. The Index of Dispersion tests whether a distribution is significantly more aggregated than a random (Poisson) distribution with the same mean (Krebs 1989). The more general Index of Crowding was also calculated, $J_A = \sigma^2/(\mu)^2 - (1/\mu)$, where σ^2 is the variance and μ is the mean of a species' distribution (Ives 1991). This measure of aggregation is not specific to a particular probability distribution, and can describe a constant density as well as aggregated distributions. A Poisson distribution has $J_A = 0$. The crowding index and negative binomial distribution are related, such that given a negative binomial distribution, $J_A = 1/k$, where k is the negative binomial's aggregation parameter. A negative binomial distribution provided a good qualitative fit for most of the aggregated distributions inspected.

The patterns of correlation between species pairs were also investigated, because positive or negative associations may exacerbate or ameliorate interspecific competition, respectively. At the scale of fruits under a single tree, larvae of different species have uncorrelated distributions for all but one of 181 possible pairwise correlations (Table 2, Bonferroniadjusted Spearman's rank correlations). At the spatial scale of trees, the mean densities of *Taeneaptera* sp. and *Richardia* sp. are positively correlated ($r^2 = 0.42$, $P = 0.014$), but all other pairwise correlations are nonsignificant (Table 2, Spearman's rank correlations). The fact that the distributions of species are generally uncorrelated or positively correlated at the scales of both fruits under a single tree and separate trees suggests that resource partitioning is not likely to be prevalent among these species, and that aggregation may be playing an important role in mediating their interactions.

The mean density of a species under different trees varied more than 20-fold (Fig. 1). The degree of aggregation, as indicated by the crowding index J_A, also varied among trees, ranging from highly aggregated to slightly more uniform than a Poisson distribution (Fig. 2). When calculated from samples of fruits under different trees, such statistics might appear to be different as a result of sampling error alone, especially if individuals are aggregated. To test whether the observed distributions of means and J_A values were different from variation due to sampling error alone, null distributions of the mean densities of each species under different trees were generated by simulating samples equal in size to the field collections. The samples were drawn from negative binomial distributions fit to the data for each species pooled over all trees. Mean and J_A values for 1000 samples were simulated.

All of the four most abundant species have distributions of means that are significantly different from the null distribution generated by sampling error (*G*-tests, P-values all < 0.01). Three of the four most

Table 1. The distributions of common *Apeiba*-feeding insects. Distributions of the four most common species, calculated separately for the fruits under each tree. The mean and J values are weighted by the number of fruits collected per tree

Species	% of trees where present	% of trees where aggregated*	Mean density (no. of fruit)	Weighted mean J (crowding index)
Taeneaptera sp.	100	96	3·38	6·38
Richardia sp.	77	67	0·74	6·43
Chlorops sp.	100	89	1·29	3·56
Tineinae sp.	97	82	0·91	5·37

*Index of Dispersion (P < 0·05).

Table 2. Correlations among species at two scales. Spearman's rank correlation coefficients for pairs of species. Values above the diagonal are means $\pm$ 1 SD at the scale of fruits under a single tree. Values below the diagonal are the correlations among mean densities at the scale of different trees

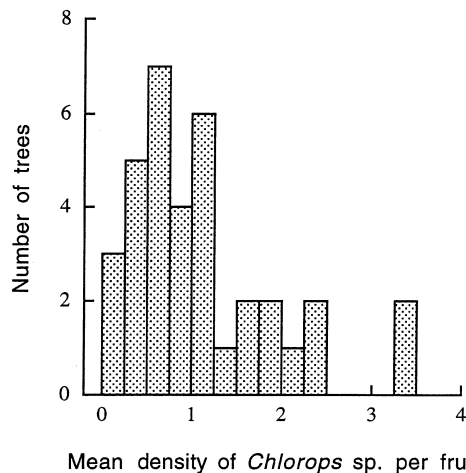| Species	*Taeneaptera* sp.	*Richardia* sp.	*Chlorops* sp.	*Tineinae* sp.
Taeneaptera sp.	1	0.30 ± 23	-0.07 ± 18	-0.09 ± 21
Richardia sp.	0·42*	1	0.05 ± 20	-0.05 ± 19
Chlorops sp.	0.16	0·01	1	0.32 ± 29
Tineinae sp.	-0.29	-0.10	-0.03	1

* $P < 0.05$.

Fig. 1. Distribution of the mean density of *Chlorops* sp. (larvae per fruit) under 28 trees. This distribution of mean densities is significantly different from a null distribution generated by random sampling (see text for details).
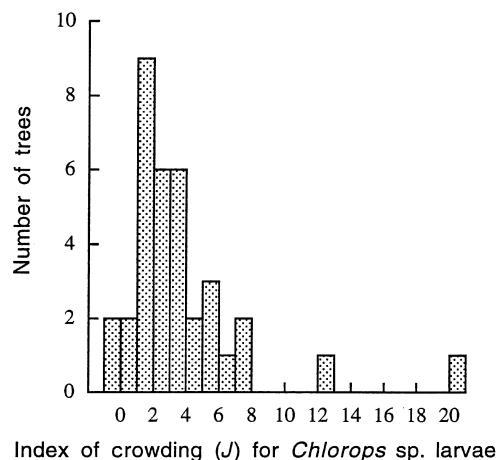

Fig. 2. Distribution of the index of crowding, J_A, for *Chlorops* sp. larvae under 28 trees. A J_A value of 0 indicates the mean and variance are equal. This distribution is significantly different from a null distribution generated by random sampling.

distributions of mean densities and J_A are significantly different from that expected due to sampling alone means that, at the scales of both trees and fruits, there is significant variation that may affect the competitive interactions of the species.

Methods

MODEL 1: EFFECTS OF AGGREGATION AT MULTIPLE SPATIAL SCALES IN A WELL-MIXED SYSTEM

To enable a comparison between the effects of aggregation at a single scale and at multiple scales, simulations presented here were based upon the structure outlined by Atkinson & Shorrocks (1981, 1984), thus incorporating the following similar assumptions. All patches are assumed to be identical in size and quality. The probability distributions for each species are used to calculate the expected frequencies of different combinations of competitors in a patch. The competitive outcome of each combination is multiplied by the expected frequency of the combination, and the results are summed over all possible combinations. This model departs from the simulations run by Atkinson & Shorrocks (1984) by including spatial variation at two scales, and by evaluating coexistence in a slightly different manner. The competition equations used to calculate the outcome of each combination of competitors will first be described, and then the method for calculating the expected frequency of different combinations. For simplicity only two species of competitors are considered, but the models can readily be extended to include many species.

THE STRUCTURE OF COMPETITION

In the models presented here there are two spatial scales at which the resource is patchy. Competition occurs within patches at the smaller spatial scale (i.e. fruits under a single tree), but patches are found within superpatches whose mean density and degree of aggregation may vary. Following Atkinson & Shorrocks (1984), the results of competition in each patch are calculated using the equations of Hassell & Comins (1976):

abundant species (all but *Taeneaptera* sp.) had J_A distributions that were significantly more variable than their null distributions based upon sampling error alone (*G*-tests, P-values < 0.01). The fact that the

$$X_{t+1} = \lambda_x X_t [1 + a_x(X_t + \alpha Y_t)]^{-b} \qquad \text{eqn 1a}$$

and

$$Y_{t+1} = \lambda_y Y_t [1 + a_y(Y_t + \beta X_t)]^{-b} \qquad \text{eqn 1b}$$

where X_t and Y_t represent the densities of the two competitors in generation t, and λ_i is the intrinsic population growth rate of species i. The parameter b describes the form of competition. When $b = 1$ the equations describe 'contest' competition, and as values of b increase, competition becomes more 'scramble' like (Hassell 1975). The carrying capacity (K) within each patch for species i in isolation is $[(\lambda_i)^{1/b} - 1]/a_i$. For this study it was assumed that the carrying capacity was identical for the two competitors, and that the species differ only in their competition coefficients (i.e. $\lambda_x = \lambda_y$, $a_x = a_y$, and b is the same for both species). Because this study was primarily interested in how aggregation of the superior competitor might facilitate persistence of an inferior competitor, it was assumed that the density of the inferior competitor does not affect the superior competitor, i.e. X represents the density of the superior competitor, and $+\alpha$ equals zero. Therefore the magnitude of β determines the strength of competition.

The frequency with which different combinations of competitors occur depends on the distributions of those competitors at each of two spatial scales, and on their covariance. It was assumed that the two species have independent distributions at both spatial scales, as had generally been observed for the *Apeiba*-feeding insects. As in previous models of aggregation-mediated coexistence, Poisson and negative binomial distributions were used to describe random and aggregated distributions of individuals, respectively (Atkinson & Shorrocks 1981, 1984; Ives 1985). The inferior competitor was assumed to follow a Poisson distribution that does not vary at the larger spatial scale, and the effect of varying only the distribution of the superior competitor at both scales was examined. Within each superpatch the superior competitor had either a Poisson or a negative binomial distribution. Previous theoretical studies have found that the distribution of the superior competitor is much more important for determining coexistence than that of the inferior competitor (Atkinson & Shorrocks 1981; Ives & May 1985; Tilman 1994).

INCORPORATING VARIATION AMONG SUPERPATCHES

The single parameter of the Poisson distribution, θ, represents both the mean and variance. The negative binomial distribution has two parameters; the mean, μ, and the degree of aggregation, k (several other parameterizations are possible, e.g. DeGroot 1986). As k is decreased from positive infinity to its lower limit of zero, the negative binomial distribution changes from an asymptotically Poisson distribution to a highly aggregated distribution.

Previous studies considered aggregation at a single spatial scale, so the parameters of probability distributions (θ, or μ and k) were constants. Some studies relaxed the assumption that k is constant and allowed k to vary as a function of the mean density (e.g. Rosewell *et al.* 1990), but all patches were still constrained to sample from a single negative binomial distribution each generation. Here, μ and k can take different values for each superpatch. In other words, the parameters are themselves random variables, drawn from probability distributions specified by hyperparameters.

It is assumed that μ and k for each superpatch are drawn from separate gamma distributions, which guarantees that they are continuous and positive. Independent distributions were assigned to μ_X and k because for most of the species in the *Apeiba* system the degree of aggregation and the mean density are uncorrelated (Inouye 1998), and for mathematical simplicity. The probability density functions (pdf) for μ_X and k are:

$$P(\mu|v_\mu, \varphi_\mu) = \varphi_\mu \mu^{\wedge}(v_\mu - 1)\,\mathrm{e}^{\wedge} - (\varphi_\mu \mu)/\Gamma(v_\mu)$$

and

$$P(k|v_k, \varphi_k) = \varphi_k k^{\wedge}(v_k - 1)\,\mathrm{e}^{\wedge} - (\varphi_k \mu)/\Gamma(v_k)$$

$$(\text{for } v \text{ and } \varphi > 0)$$

where Γ is the gamma function. The means are v_μ/φ_μ and v_k/φ_k, and variances are v_μ/φ_μ^2 and v_k/φ_k^2. The parameters can be changed independently to represent a wide range of distributions, from skewed (cf. Figs 1 and 2.) to nearly symmetric. For all simulations a constant ratio of the variance to the mean was used for the gamma distributions of μ and k, rather than a constant variance, because the mean changes over the course of the simulation. For the gamma distribution, the variance to mean ratio is equal to the inverse of the shape parameter ($1/\varphi$).

Because competition occurs at the smaller, within-patches scale, the distribution of individuals is calculated at this scale, given a probability distribution with parameters that vary among superpatches. This is equivalent to finding the marginal distribution of individuals at the smaller scale by integrating the probability distribution with respect to its variable parameters. The pdf for a Poisson distribution is $P(y|\theta) = \theta^y\,e^{-\theta}/y!$, where y is the number of competitors per patch. For a Poisson distribution with parameter θ, when θ has a gamma (v_θ, φ_θ) distribution, the appropriate integral is $\int_0^\infty P(y|\theta)\ P(\theta|v_\theta, \varphi_\theta)\ d\theta$. After integration and some simplification the result can be recognized as a negative binomial distribution with parameters $\mu = v_\theta/\varphi_\theta$ and $k = (\varphi_\theta + v_\theta)/(\varphi_\theta + 1)$ (Gelman *et al.* 1995). Thus, if the superior competitor has a random distribution within each superpatch (e.g. tree), but also has a variable rate parameter (e.g. the

mean density varies among trees), then the marginal distribution is not Poisson but negative binomial.

The integral of a negative binomial distribution with respect to its gamma-distributed parameters has no known closed form solution. The marginal distribution for the negative binomial was therefore calculated using numerical simulation. The approach was to draw values for μ_X and k from their respective gamma distributions, and then draw the number of individuals in a patch from a negative binomial distribution with the chosen μ_X and k. The negative binomial distribution was truncated at 20 times the patch carrying capacity, where the distribution's tail is negligible. This process was then repeated at least 3000 times to estimate the shape of the marginal distribution for each generation.

The marginal distribution obtained by integrating over variable parameters represents the distribution of individuals over all patches, given the assumption that there is complete mixing among superpatches every generation. If only some individuals disperse among superpatches, then the distribution of individuals in the next generation is an admixture of the marginal distribution due to mixing and local distributions due to processes within each superpatch. The assumption of complete mixing is relaxed in model 2.

The present study assumed that the superior competitor is unaffected by the inferior competitor (equation 1), thus similar distributions of the superior competitor are recreated every generation, and coexistence criteria are the same every generation. Because the mean density of the superior competitor affects the survival of the inferior competitor, the maximum value of the competition coefficient (β) was calculated that would allow the inferior competitor to increase from a low density, when the superior competitor was at its equilibrium density. An under-appreciated consequence of aggregation is that the equilibrium density of a species decreases as the degree of aggregation of that species increases (Hanski 1981). Figure 3 shows the relationship between the equilibrium density of a single species and its degree of aggregation (using equation 1). The equilibrium mean density among patches is lower than the carrying capacity, and only asymptotically approaches the carrying capacity as the distribution of individuals becomes random. Therefore the model was run with only the superior competitor present until it reached its equilibrium. When the superior competitor reached its equilibrium density the inferior competitor was introduced, following a Poisson distribution with a mean density of 1% of the single-species carrying capacity. The study then solves for the maximum value of β that gave the inferior competitor a positive population growth rate. Although it is theoretically possible for there to be a stable equilibrium where the inferior competitor has a density less than 1% of its single-species carrying capacity, such a low-density popu-
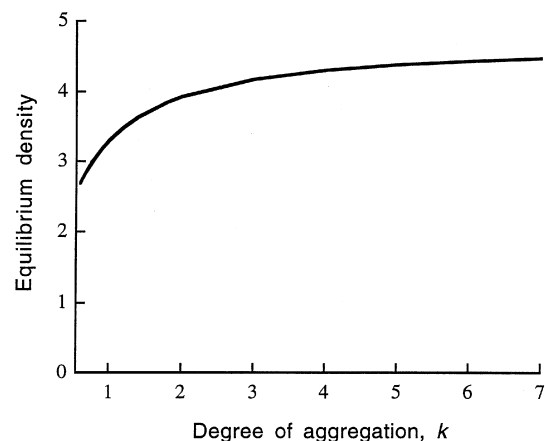

Fig. 3. Aggregation depresses the single-species equilibrium density below the per patch carrying capacity in a nonlinear fashion. As k approaches infinity the equilibrium density asymptotically approaches the carrying capacity ($K = 5$).

lation would probably not be viable in nature, unless the carrying capacity were extremely large.

To find the maximum value of β allowing an increase in the density of the inferior competitor (β_{max}), the competition equation was rewritten for the inferior competitor to represent patches with different densities, and then the Van Wijngaarden–Dekker–Brent method was used (Press *et al.* 1989) to solve numerically for β, such that the population growth rate of the inferior competitor was zero (i.e. $Y_t = Y_{t+1}$). Specifically, equation 1b can be rewritten with X and Y as probability vectors, and expressed as:

$$0 = \Sigma_y \Sigma_x \{ y \, [\lambda(1 + a_y(y + \beta x))^{-b} - 1] \, P(y)P(x) \}$$

where $P(y)$ and $P(x)$ are the marginal probabilities of observing y or x individuals of species Y or X, respectively, in a patch. This equation has only one real root for β (β_{max}), because the equilibrium for equation 1 (a, b) is globally stable (Hassell & Comins 1976). For any value of β above this root the inferior competitor decreases in abundance. For values of β below this root the inferior competitor increases in density until it has reached its own equilibrium. Because the inferior competitor does not affect the population dynamics of the superior competitor, this method will find any equilibrium for the inferior competitor that is greater than its initial density.

MODEL 2: ADDING MOVEMENT AMONG SUPERPATCHES

Model 2 relaxes the assumption of model 1 that there is global dispersal among superpatches. Otherwise the structure of the two models is similar. Limited movement is incorporated by allowing a fraction, γ, of individuals to leave their natal superpatch and enter a pool of dispersers. The pool of dispersing individuals is then divided equally among superpatches. Thus, movement is described by the equation

$X_{i,a} = \gamma X_{*,b} + (1-\gamma) X_{i,b}$, where $X_{i,a}$ is the density of individuals in superpatch i after dispersal, $X_{*,b}$ is the mean density over all superpatches, and $X_{i,b}$ represents the density of individuals in superpatch i before dispersal. An analogous equation describes movement for the second species. To avoid confounding the effects of variation in aggregation among superpatches with effects of the fugitive species mechanism for coexistence (Horn & MacArthur 1972), where coexistence is a result of differences in movement rates, both species are assigned identical values of γ.

In model 2 the superior competitor was distributed among patches within a superpatch according to a negative binomial distribution. The distribution of the inferior competitor within superpatches was Poisson. The outcome of competition in each patch was calculated using the same Hassell and Comins competition equations (Hassell & Comins 1976) as for model 1 (equation 1), with the parameter $b = 1$. Variation in the degree of aggregation among superpatches was represented by assigning each superpatch a different value of k, randomly drawn from a gamma distribution. The value of k for a superpatch was assigned at the beginning of each simulation and did not change across generations. Unlike model 1, there was no intrinsic variation in mean density that was recreated each generation. This does not mean that μ_X and μ_Y were necessarily constant. Variation in mean densities is a potential consequence of variation in k at low movement rates.

Simulations for model 2 were started with the superior competitor near its equilibrium density by simulating several generations before introducing the inferior competitor; otherwise transient patterns in the dynamics of the competitors could appear. The inferior competitor was introduced at 1% of its single-species carrying capacity. The simulation kept track of 100 superpatches. For each generation, the competition equations were iterated, taking into account all possible combinations of competitors within each superpatch and the expected frequencies of those combinations. Competition was followed by movement and reproduction of survivors, if γ is nonzero. For simplicity, the hyperparameter φ_k from the Gamma distribution of k-values was set equal to one. The structure of this model is similar to that of many simple metapopulation models (Kareiva 1990; Hastings & Harrison 1994). From the perspective of the inferior competitor superpatches vary in quality as a result of differences in the degree of aggregation of the superior competitor.

Because of limited movement among superpatches and variation in k, the distributions of superior competitors differed among superpatches, and thus β_{max} differed among superpatches. Therefore, in model 2 the criterion for coexistence was based not on β_{max} but on the number of generations until the mean density per patch of the inferior competitor fell below a minimum threshold (0·2% of K) in every superpatch, as a

function of β and γ. The simulations were run until it was clear that the inferior competitor would increase in density, go globally extinct, or persist in some superpatches and go locally extinct in others.

Results

MODEL 1

The maximum competition coefficient that will allow the inferior competitor to increase from an initially low density depends on the distribution of the superior competitor. As noted above, a Poisson distribution of the superior competitor with parameter θ, when θ has a gamma(v_θ, φ_θ) distribution, has a marginal negative binomial distribution. This means that the results of previous studies using negative binomial distributions at a single scale are applicable. The effect of changing the mean degree of aggregation, k, on β_{max}, the maximum intensity of competition allowing coexistence, is shown by the solid curve in Fig. 4. Coexistence is possible for all values of β below this line.

A negative binomial distribution with variable parameters has a marginal distribution that looks very similar to another negative binomial distribution, but the present study could not prove them to be equivalent. Because of nonlinear relationships between k, the mean, μ and variance, the marginal distribution of a negative binomial distribution with variable parameters is more leptokurtic and has higher variance
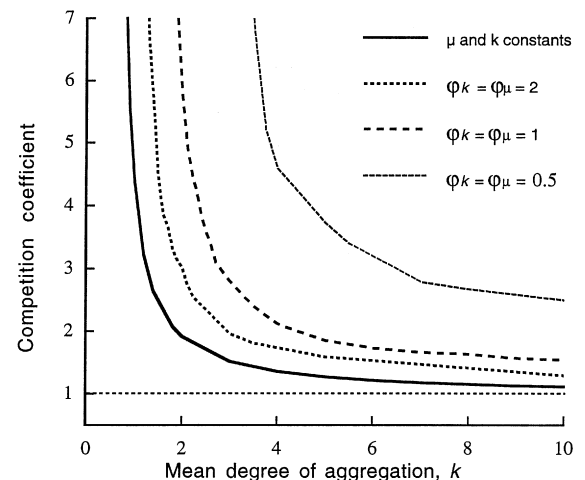

Fig. 4. β_{max} as a function of the mean degree of aggregation of the superior competitor. The horizontal line at 1 is the value of β_{max} if the superior competitor is not aggregated. The solid curve shows values of β_{max} for a superior competitor with a negative binomial distribution. The upper curves show values of β_{max} when the superior competitor has a negative binomial distribution with parameters that are gamma distributed variables, with hyperparameters φ_μ and φ_k equal to 2, 1 or 0·5 (i.e. variance : mean ratio of 0·5, 1 or 2). The hyperparameters v_μ and v_k help to determine the mean degree of aggregation. For both species $\lambda = 4$, $a = 0·8$, and $b = 1$ (equation 1).

than a negative binomial distribution with constant parameters which are equal to the means of the variable parameters. Figure 4 shows that for any given mean value of k, $\beta_{\max}$ increases as the degree of variability of μ_X and k increases (i.e. as φ_μ and φ_k decrease).

Variation in μ_X does not affect $\beta_{\max}$ in the same way as variation in k (Fig. 5) because these parameters change the marginal distribution of individuals in different ways. Variation in k among superpatches with a constant mean has practically no effect on $\beta_{\max}$ when the mean value of k is relatively high, but variability in k strongly increases $\beta_{\max}$ when the mean value of k is small. This is despite the fact that the absolute variance of k is smaller when the mean is small, because the variance to mean ratio is held constant. Keeping k constant but making the mean variable has an appreciable effect on $\beta_{\max}$ at all values of k.

Simulations showed that the scaling parameter b from the Hassell and Comins competition equations has very little effect on $\beta_{\max}$, and then only when individuals are highly aggregated (i.e. $k < 1$, results not shown). This is because the outcome of scramble and contest competition only differs at high densities (Hassell 1975). The effect of higher values of b (i.e. more scramble-like competition) is to increase $\beta_{\max}$ for a given k, but only by a very small amount.

The results shown in Figs 4 and 5 were also robust to changes in the density at which the inferior competitor was introduced (results shown are for an initial density of 1% of K). Simulations were run in the present study in which the inferior competitor was introduced at 0·02%, and 2% of the single-species patch carrying capacity. Introducing the inferior competitor at 0·02% of K did not change the qualitative relationship
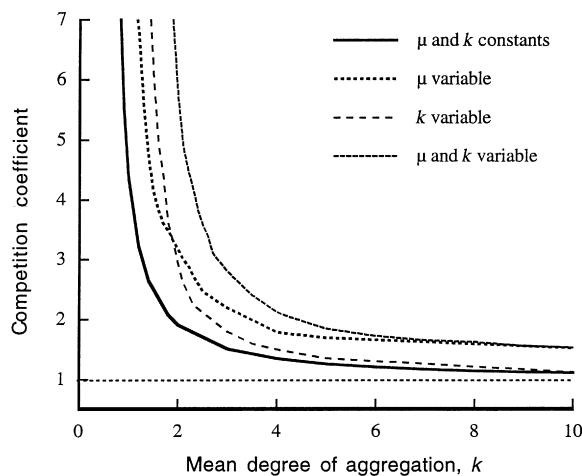
between k and $\beta_{\max}$, but increased $\beta_{\max}$ nearly uniformly by $\approx 6\%$ (other parameters the same as in Figs 4, 5). When the inferior competitor was introduced at 2% of K, $\beta_{\max}$ was decreased by $\approx 3\%$, however, the decrease in $\beta_{\max}$ was slightly less at high values of k and slightly more at lower values of k ($k << 2$).

MODEL 2

When the movement parameter γ is equal to 1 (Fig. 6c), which represents complete mixing every generation, the two models are similar and provide qualitatively similar results. As the superior competitor becomes more aggregated (lower values of k), coexistence becomes possible for larger values of $\beta_{\max}$, and the inferior competitor persists for more generations.

Fig. 5. Variation in the parameters μ and k has separate effects. The horizontal line is as in Fig. 4. The solid curve shows values of $\beta_{\max}$ for a superior competitor with a negative binomial distribution and both parameters constant. If variable, the hyperparameters φ_μ and φ_k are equal to 1. The hyperparameters v_μ and v_k help to determine the mean degree of aggregation.
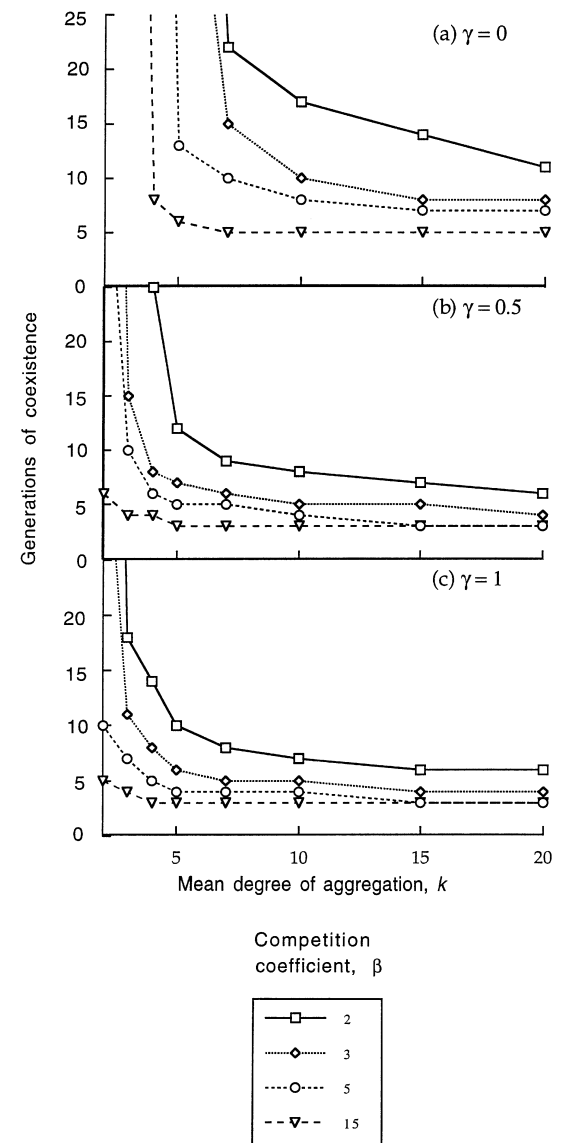

Fig. 6. The rate of movement among superpatches changes the number of generations that the competitors can coexist for given values of k and β.

This paper shows the results for only a single threshold density for persistence, 0·2% of K (Fig. 6). Decreasing the threshold density to 0·1% or 0·05% of the single-species carrying capacity did increase the number of generations that the inferior competitor can persist, but it did so for all movement rates, and did not alter the qualitative effect of movement on generations of coexistence or other results. The results presented here were calculated with $\varphi_k = 1$; changes in φ_k had little effect (results not shown).

EFFECT OF MOVEMENT ON THE PERSISTENCE OF THE INFERIOR COMPETITOR

Overall, increasing the rate of movement among superpatches (increasing γ) decreased the number of generations that the superior and inferior competitors coexist (Fig. 6). For high values of k, lower rates of movement increased the number of generations that the inferior competitor can persist, but only by a few generations. At low values of k restricted movement strongly increased persistence, and a small change in γ could make the difference between rapid extinction and indefinite coexistence. Only for a small range of parameters when movement was limited (γ near 0) was it possible to have the inferior competitor persist in some superpatches and remain practically absent from others.

NO MOVEMENT BETWEEN SUPERPATCHES

In the absence of movement among superpatches ($\gamma = 0$), the individuals in different superpatches constitute independent populations. Each population of the inferior competitor either went extinct or reached an equilibrium value, depending on the degree of aggregation of the superior competitor in that superpatch. This means that the inferior competitor sometimes had a relatively high regional density averaged over all superpatches, and yet was extinct in most. In this case only one or a few superpatches were responsible for the survival of the inferior competitor, and loss of those few superpatches would cause regional extinction. Whether or not the inferior competitor persisted depended on the superior competitor's minimum value of k over all superpatches. In theory, if there were an infinite number of superpatches and a continuous distribution of k-values for those superpatches, then there would always be some (perhaps very small) fraction of the superpatches where the inferior competitor could persist. But in reality, the distribution of k-values will have finite tails, and there is always a finite number of superpatches. This is what allowed global loss of the inferior competitor in simulations even when there was no movement (e.g. at high values of β and k, Fig. 6a).

EFFECT OF MOVEMENT ON THE VARIANCE OF MEAN DENSITIES AMONG SUPERPATCHES

In model 1 a superior competitor with a negative binomial distribution was considered in which one or both of the parameters μ_X and k were variable. When these parameters were both variable they were assigned independently. In model 2 intrinsic variation in k only was assumed, but that did not mean that μ_X was constant among superpatches. Instead, the distributions among superpatches of μ_X and μ_Y, the mean densities per superpatch of the superior and inferior competitors, respectively, could change over time. Thus, rather than assuming variation in μ_X existed, in model 2 variation in μ_X could arise as a consequence of intrinsic variation in k only. An understanding of variation in μ_X helps to explain the mechanism by which variation in k in model 2 promotes coexistence. This may also be helpful for investigating the effects of movement in field-collected data, as many data sets show correlations between the mean density and the degree of aggregation (Taylor, Woiwood & Perry 1979; Rosewell *et al.* 1990).

When the rate of movement among superpatches was high, the variance in both μ_X and μ_Y was low (Fig. 7). At the extreme ($\gamma = 1$), the density in all superpatches was reset to the global mean density every generation. The variance in μ_X and μ_Y increased more slowly with decreased movement when the mean value of k was high, i.e. when the superior competitor was not highly aggregated on average; for example, when k was greater than 4, the coefficient of variation in μ_X and μ_Y was always less than 0·05 (cf. Figure 7). Dependence on k arose because of the nonlinear relationship between k and the equilibrium density of the superior competitor (Fig. 3). The variance in μ_Y depended directly on the distribution of the superior competitor as measured by k; recall that the distribution of the inferior competitor was Poisson.
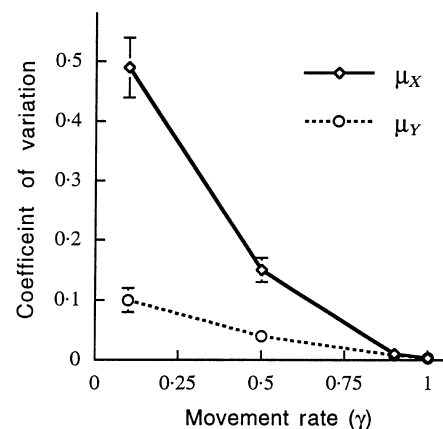

Fig. 7. In model 2, the coefficient of variation (CV) of the mean densities of competitors among superpatches depends on the rate of movement among superpatches. Error bars represent ± 1 SE of the CV. X denotes the superior competitor. ($\beta = 2$, mean $k = 3$, $\varphi_X = 1$).

Because the variance in μ_X was a result of variance in k, when there was little movement among superpatches μ_X, μ_Y and k became highly correlated within a few generations. For the superior competitor, μ_X and k were positively correlated ($\rho \approx 0.8$ for the simulations described above), whereas for the inferior competitor μ_Y was always negatively correlated with k (ρ depended nonlinearly on γ, and ranged from -0.15 to -0.85). However, when either the movement rate or k was high, the correlations between μ_X, μ_Y and k were not significantly different from zero because the total variance in μ_X and μ_Y was extremely small.

Discussion

The distributions of competitors can have aggregated patterns at more than one spatial scale. For fruit-feeding insects, trees and their fruits are an obvious case of patches nested within superpatches. Animal dung is another example of a patchy and ephemeral resource that supports diverse insect communities (reviewed in Hanski 1990), and can be patchy at two scales. Each pile of dung is a discrete patch at a smaller spatial scale, while different social groups or pastures might represent superpatches. This pattern may also be found in plant–insect systems, where individual host plants are found within larger patches (e.g. disturbed areas, tree-fall gaps, etc.). In some systems there may even be relevant spatial patterns at more than two scales. Debouzie & coauthors (1993, 1996) investigated spatial patterns for weevils at four nested scales, from patches of trees down to individual nuts within a husk, and found significant intraspecific aggregation at three of these scales.

Since spatial patterns can be measured at multiple scales, understanding the regional coexistence of competitors will require an understanding of the effects of spatial variation at multiple scales; for example, Atkinson & Shorrocks (1984) and Ives & May (1985) showed that patchiness will not promote coexistence of competitors if the superior competitor has a Poisson distribution within a single superpatch. However, if the mean densities vary among superpatches, then the marginal distribution of competitors among all patches has an aggregated, rather than Poisson, distribution (e.g. Jaenike 1994). This degree of aggregation might be sufficient to allow regional coexistence, when, on average, the distribution within any one superpatch would not. This scenario, in which aggregation is a product of variation at two scales, represents one point on a continuum of spatial patterns. At one extreme, there may be no variation within superpatches but marked aggregation among superpatches. At the other extreme, the distribution within each superpatch may be aggregated, while superpatches do not vary.

In the following sections the importance of integrating variation in density and aggregation at multiple spatial scales for understanding mechanisms of coexistence is discussed. First well-mixed cases will be discussed, in which the marginal distribution is an appropriate representation of the distribution of competitors over all patches. This approach has implications for how field data should be collected, and for how spatial variation is represented in theoretical investigations. The amount of movement among superpatches will also determine the regional distribution of competitors, and thus influence their coexistence. Finally there is an exploration of how movement rates might be incorporated into an understanding of how spatial patterns at multiple scales combine to determine coexistence.

DESCRIBING SPATIAL AGGREGATION AS A FUNCTION OF PROCESSES AT TWO SCALES

Many organisms have different types or timescales of behaviours at different spatial scales. For the guild of *Apeiba*-feeding insects that motivated the models in this paper, competition probably occurs only among larvae, which complete their development within a single fruit. It is unlikely that these insects compete at the larger scale of trees, but potentially important spatial variation is created by the behaviours of adult insects, which fly among trees. Thus at a small scale one might study certain interspecific interactions, whereas at a larger scale one might concentrate on the preferences and behaviours of adults that influence their distribution among trees or forest types. While each of these studies can profitably address questions at an appropriate single scale, any study that attempts to address issues involving phenomena at multiple scales, such as studies of regional population dynamics or coexistence, must explicitly consider all relevant scales.

One promising way to describe explicitly processes at multiple nested scales is demonstrated in this paper. Rather than keep track of every individual in a spatially explicit description, variation among small-scale patches was represented by probability distributions, and the parameters of these distributions were made variables in order to describe large-scale variation among superpatches. Similarly, in a model of host–parasitoid interactions, May (1978) justified his use of a negative binomial distribution of parasitoid attacks using a Poisson distribution with variable mean, however, he did not specify a distribution for the mean. Calculating a marginal distribution by integrating out the variation at one scale provides a description of the regional pattern of spatial variation, and takes into account the variation present at both scales. Ignoring the variation among superpatches by using only mean values of the parameters that dictate the distribution of competitors within a superpatch will give incorrect predictions whenever the predictors of interest (e.g. β_{max}) are nonlinearly related to the parameters. The reason is that Jenson's inequality (which states that the mean of a function is not equal to the function of

the mean) applies to the results of both the models presented above.

The effects of changes in the mean density and degree of aggregation (μ_X and k) on the ability of competitors to coexist are strongly nonlinear. Figure 5 shows that, for a negative binomial distribution, when μ_X is held constant and k is variable the effect on β_{max} depends on the mean value of k. At higher values of k, variance in k has almost no effect on β_{max}. This is because at high values of k the relationship between k and β_{max} is nearly linear (as shown by the line for constant μ_X and k in Figs 4, 5). As k gets smaller and the relationship between k and β_{max} becomes more nonlinear, variation in k has a larger effect on β_{max}. Making μ_X variable increases β_{max} for a different reason. Recall that as k gets larger a negative binomial distribution converges asymptotically to a Poisson distribution. Adding variance to the mean of a Poisson distribution skews its marginal distribution and increases its overall variance (Jaenike 1994). The same result occurs when the mean of the negative binomial distribution varies, and this effect remains important even when k is large.

METHODOLOGICAL IMPLICATIONS

The results of model 1 demonstrate that incorporating spatial variation at two nested scales can change the predicted outcome of competition between two species. This implies that field data should be collected in a spatially structured manner, and that it should be analysed in a way that does not ignore variation at all but one scale. An alternative methodological approach that would avoid using hyperparameters would be to ignore variation among superpatches (e.g. trees) and estimate the overall distribution of individuals based on a random sample of patches (e.g. fruits). A truly random sample would provide an unbiased estimate of the marginal distribution, but there are at least three problems with this approach. The first problem is that it ignores information about the biological processes that act at the different scales, which is potentially useful for generating hypotheses about the natural history responsible for spatial patterning. The second problem is a practical one, which is that a truly random sample is difficult to collect unless all superpatches are identified. A sampling regime that first selects a random set of superpatches, and then samples only from within those superpatches, will yield an estimate of the marginal distribution that is biased and has large sampling error. If only some superpatches are available, then it is more parsimonious to sample from these, estimate the variance among superpatches, and assume that unsampled patches have a similar distribution of parameters. Third, using a single random sample is not appropriate if movement is restricted, so that competition is influenced more by the local distribution than the regional distribution of competitors.

For theoretical investigations, the approach of explicitly including variation by integrating over hyperparameters is widely applicable, provided that the rate of movement among superpatches is high. The models described in this paper used numerical simulation and analytical methods. The flexibility of the gamma distribution means that the results presented here are fairly general, but data from a natural system may have a bimodal distribution, or other features that prevent use of a standard distribution. In situations where one needs to combine unusual distributions or sample from empirical distributions of data, a Markov chain Monte Carlo (MCMC) approach is likely to be useful (Gilks *et al.* 1996).

LIMITED MOVEMENT AMONG SUPERPATCHES

The results of model 2 (Fig. 6) show that the number of generations that the inferior competitor can persist is, in part, dependent on the rate of movement among superpatches. If individuals do not freely mix among all patches, then their marginal distribution, as calculated in model 1, will underestimate the regional spatial variation in competitor density experienced by individuals. This means the marginal distribution provides the minimum effect of spatial variation at multiple scales for promoting coexistence of competitors. This holds for the case in which the superior competitor has a Poisson distribution within superpatches and there is variation in θ among superpatches (results not shown), as well as for the case presented in model 2, where the parameter k of the negative binomial distribution is variable. In both cases limited movement promotes coexistence because it affects the rate of mixing between population sources and population sinks for the inferior competitor (Pulliam 1988; Doak 1995). In the first case, that of variation in the Poisson parameter θ, superpatches in which the superior competitor is present at a low density (low θ) represent source populations for the inferior competitor, while sinks occur where the superior competitor is at a high density. In the case of variation in the negative binomial parameter k, populations of the inferior competitor are sources where the superior competitor is highly aggregated, and sinks where the superior competitor is weakly aggregated. The effects of movement on the coexistence of the competitors in model 2 are based on the assumption that the value of k for each superpatch does not change over time. Thus, each superpatch has a stable equilibrium mean density based on the within-superpatch distribution and migration. If the values of k were changed every generation, then the effects of movement might be altered.

In model 2, low movement rates among superpatches also had the potential to create variation in μ_X and μ_Y among superpatches, and this variation was correlated with the value of k for the superior competitor. Taylor, Woiwod & Perry (1978, 1979) and

Rosewell *et al.* (1990) observed that in many data sets there is a correlation between the mean density in a patch and the degree of aggregation as measured by *k*, and that this correlation (when present) could be positive or negative. The results of model 2 suggest a mechanism for creating a correlation between μ and *k*, if different species have correlated values of *k* in each superpatch. Furthermore, the sign of a correlation between μ and *k* would depend on the structure of competitive interactions. For most species of insects that live in *Apeiba* fruits the within-tree distribution of larvae is significantly aggregated, yet the mean density of larvae is not significantly correlated with the degree of aggregation under each tree (Inouye 1998). This suggests that the significant variation in mean densities observed in this system are not due solely to limited movement among trees combined with fixed spatial variation in aggregation. Other characteristics of either the trees or their locations probably also influence the mean densities of these insects.

Decreasing the rate of movement among superpatches promotes coexistence of the inferior competitor in part because, as discussed above, variance in the mean density of the superior competitor is maintained at low movement rates. This spatial variance in μ_X among superpatches also promotes coexistence, as shown by model 1 (Fig. 5). In model 2 μ_X and *k* are not independent (unlike model 1), however, the effect of variation in the mean density will be qualitatively similar.

Conclusions

Adding variance at a larger spatial scale increases the variance among all patches, and has the effect predicted by Ives & May (1985) of promoting the coexistence of competitors. What the simulations discussed in this paper show is that the relative importance of variation at each of two scales can differ. For insects that use rotting fruits as a resource there are two obvious spatial scales to consider. Even though the spatial variance measured at either the scale of fruits under a single tree, or of variation among trees, might be insufficient to allow the coexistence of competitors, a regional distribution that includes variation at both scales may permit coexistence. Evaluating the importance of different spatial scales in natural systems will require measuring aggregation at the appropriate scales, as well as knowledge of the within-patch interactions among competitors. In cases where movement among superpatches is limited, regional population dynamics will be a mixture of small-scale processes and large-scale patterns of movement.

References

Atkinson, W.D. & Shorrocks, B. (1981) Competition on a divided and ephemeral resource: a simulation model. *Journal of Animal Ecology*, **50**, 461–471.

Atkinson, W.D. & Shorrocks, B. (1984) Aggregation of larval Diptera of discrete and ephemeral breeding sites: the implications for coexistence. *American Naturalist*, **124** (3), 336–351.

Chesson, P.L. & Warner, R.R. (1981) Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist*, **117**, 923–943.

Debouzie, D., Heizmann, A. & Humblot, L. (1993) A statistical analysis of multiple scales in insect populations. A case study: the chestnut weevil *Cucurlio elephas*. *Journal of Biological Systems*, **1**, 239–255.

Debouzie, D., Heizmann, A., Deshouhant, E. & Menu, F. (1996) Interference at several temporal and spatial scales between two chestnut insects. *Oecologia*, **108**, 151–158.

DeGroot, M. (1986) *Probability and Statistics*. Addison-Wesley, Reading, MA.

Doak, D.F. (1995) Source-sink models and the problem of habitat degradation: general models and applications to the Yellowstone Grizzly. *Conservation Biology*, **9**, 1370–1379.

Gelman, A., Carlin, J.B., Stern, H.S. & Rubin, D.B. (1995) *Bayesian Data Analysis*. Chapman & Hall, New York.

Gilks, W.R., Richardson, S. & Speigelhalter, D.J. (1996) *Markov Chain Monte Carlo in Practice*. Chapman & Hall, New York.

Gross, K.L., Pregitzer, K.S. & Burton, A.J. (1995) Spatial variation in nitrogen availability in three successional plant communities. *Journal of Ecology*, **83**, 357–367.

Hanski, I. (1981) Coexistence of competitors in patchy environment with and without predation. *Oikos*, **37**, 306–312.

Hanski, I. (1990) Dung and carrion insects. *Living in a Patchy Environment* (eds B. Shorrocks & I. R. Swingland), pp. 127–145. Oxford University Press, Oxford.

Hassell, M.P. (1975) Density-dependence in single species populations. *Journal of Animal Ecology*, **44**, 283–295.

Hassell, M.P. & Comins, H.N. (1976) Discrete time models for two-species competition. *Theoretical Population Biology*, **9**, 202–221.

Hastings, A. & Harrison, S. (1994) Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics*, **25**, 167–188.

Horn, H.S. & MacArthur, R.H. (1972) Competition among fugitive species in a harlequin environment. *Ecology*, **54**, 749–752.

Inouye, B.D. (1998) *The role of aggregation at nested spatial scales for the coexistence of competitors* PhD thesis, Duke University, NC, USA.

Ives, A.R. (1988) Aggregation and the coexistence of competitors. *Annales Zoologica Fennici*, **25**, 75–88.

Ives, A.R. (1991) Aggregation and coexistence in a carrion fly community. *Ecological Monographs*, **61**, 75–94.

Ives, A.R. & May, R.M. (1985) Competition within and between species in a patchy environment: relations between microscopic and macroscopic models. *Journal of Theoretical Biology*, **115**, 65–92.

Jaenike, J. (1994) Aggregations of nematode parasites within *Drosophila*: proximate causes. *Parasitology*, **108**, 569–577.

Kareiva, P. (1990) Population dynamics in spatially complex

environments: theory and data. *Philosophical Transactions of the Royal Society of London B*, **330**, 175–190.

van Klinken, R.D. & Walter, G.H. (1996) The ecology of organisms that breed in a divided and ephemeral habitat: insects of fallen rainforest fruit. *Acta Oecologia*, **17**, 405–420.

Krebs, C.J. (1989) *Ecological Methodology*. HarperCollins, New York.

May, R.M. (1978) Host–parasitoid systems in patchy environments: a phenomenological model. *Journal of Animal Ecology*, **47**, 833–843.

Press, W.H., Flannery, B.P., Teukolsky, S.A. & Vetterling, W.T. (1989) *Numerical Recipes in Pascal: The Art of Scientific Computing*. Cambridge Press, New York.

Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **137**, 652–661.

Rosewell, J., Shorrocks, B. & Edwards, K. (1990) Competition on a divided and ephemeral resource: testing the assumptions. I. Aggregation. *Journal of Animal Ecology*, **59**, 977–1001.

Sevenster, J.G. (1996) Aggregation and coexistence. I. Theory and analysis. *Journal of Animal Ecology*, **65**, 297–307.

Shorrocks, B. (1990) Coexistence in a patchy environment.

Living in a Patchy Environment (eds B. Shorrocks & I. R. Swingland), pp. 91–106. Oxford University Press, Oxford.

Shorrocks, B. & Bingley, M. (1994) Priority effects and species coexistence: experiments with fungal-breeding Drosophila. *Journal of Animal Ecology*, **63**, 799–806.

Shorrocks, B., Rosewell, J. & Edwards, K. (1990) Competition on a divided and ephemeral resource: testing the assumptions. II. Association. *Journal of Animal Ecology*, **59**, 1003–1017.

Taylor, L.R., Woiwod, I.P. & Perry, J.N. (1978) The density-dependence of spatial behavior and the rarity of randomness. *Journal of Animal Ecology*, **47**, 383–406.

Taylor, L.R., Woiwod, I.P. & Perry, J.N. (1979) The negative binomial as a dynamic ecological model for aggregation, and the density dependence of k. *Journal of Animal Ecology*, **48**, 289–304.

Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.

Underwood, A.J. & Chapman, M.G. (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia*, **107**, 212–224.