SPECIAL TOPIC: SCALING-UP IN ECOLOGY

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Scaling up from local competition to regional coexistence across two scales of spatial heterogeneity: insect larvae in the fruits of *Apeiba membranacea*

Abstract Species that live in patchy and ephemeral habitats can compete strongly for resources within patches at a small scale. The ramifications of these interactions for population dynamics and coexistence at regional scales will depend on the intraspecific and interspecific distributions of individuals among patches. Spatial heterogeneity due to independent aggregation of competitors among patchy habitats is an important mechanism maintaining species diversity. I describe regional patterns of aggregation for four species of insect larvae in the fruits of *Apeiba membranacea*, a Neotropical rainforest tree. This aggregation results from variation in densities at a small scale (among the fruits under a single tree), compounded by significant variation among trees in both mean densities and degrees of aggregation. Both the degrees of aggregation and mean densities are statistically independent within and across species at both spatial scales. I evaluate the regional consequences of these spatial patterns by using maximum likelihood methods to parameterize a model that includes both explicit measures of the strength of competition and spatial variation at both within- and among-tree spatial scales. Despite strong competitive interactions among these species, during 2 years the observed spatial variation at both scales combined was sufficient to explain the coexistence of these species, although other coexistence mechanisms may also operate simultaneously. The observed spatial variation at small spatial scales may not be sufficient for coexistence, indicating the importance of considering multiple sources of spatial heterogeneity when scaling up from experiments that investigate local interactions to regional patterns of coexistence.

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Introduction

A major goal of community ecology is to explain the maintenance of species diversity. Communities of species using patchy and ephemeral habitats (such as dung, carrion, mushrooms, rotting fruits, or tree-fall gaps) have received particular attention because they tend to be unusually diverse, but particularly high levels of resource partitioning in such habitats seems unlikely (Elton 1966; Hanski 1990). In these communities high regional diversity is likely to be due in part to processes manifest at larger spatial scales, because each local community within a single patch is by definition ephemeral and thus unstable over time-scales longer than one or at most a few generations. It is often not feasible to conduct experiments at the larger spatial scales that would be appropriate for testing regional mechanisms of coexistence, but small-scale experiments with local communities can be combined with data on regional patterns of species distributions in order to scale up from local interactions to inferences about regional outcomes.

In patchy communities individuals can interact strongly with other individuals that share the same patch, but not at all with individuals in other patches. If habitat patches are also ephemeral then the consequences of these local interactions at a regional scale (over an ensemble of local habitat patches) depend on how individuals of different species are distributed among all the patches in a region (see Melbourne and Chesson 2005 for single-species consequences of spatial heterogeneity). The independent aggregation of competitors among patches can allow the regional

coexistence of even strongly competing species (Atkinson and Shorrocks 1981, 1984; Hanski 1981). The regional outcome of this mechanism for coexistence depends on both the degree of aggregation among patches and the strength of competition within patches. Scaling up from knowledge of local (within patch) interactions to patterns of regional coexistence attributable to the aggregation mechanism requires information about regional (among patch) intraspecific aggregation and interspecific covariances in species' distributions.

Previous studies have measured aggregation for insect communities in mushrooms (Jaenike and James 1991; Heard 1998; Wertheim et al. 2000), carrion (Ives 1991; Woodcock et al. 2002), and rotting fruits (Rosewell et al. 1990; Sevenster and van Alphen 1996; Krijger 2000). All of these studies have found that the average degree of intraspecific aggregation is relatively high, and conclude that aggregation is promoting coexistence, despite competition for resources within patches (e.g. Grimaldi and Jaenike 1984; Ives 1991; Sevenster 1992). However, even statistically significant aggregation may not be sufficient to allow coexistence by itself if interspecific competition is sufficiently strong. Using assumptions about the relationship between equilibrium densities and competitive ability, Sevenster (1996) derived a persistence criterion that depends only on the aggregation of the superior competitor and covariances of interspecific densities. This persistence criterion appears to be very useful for communities of *Drosophila* (Wertheim et al. 2000; Krijger and Sevenster 2001), but its applicability to more diverse communities is untested. There have been relatively few other empirical studies that address the relative importance of coexistence mechanisms for patchy and ephemeral habitats in the field (but see Ives 1991; Marino 1991a, b; Sevenster 1992; Krijger 2000).

It has been noted that in many systems the total degree of aggregation may depend on processes at more than one spatial scale (Debouzie et al. 1996; Underwood and Chapman 1996; Krijger and Sevenster 2001). For example, from the perspective of insects that use rotting fruits, each fruiting tree is a patch at one scale, and individual fruits are patches at a smaller nested spatial scale. Inouye (1999a) used a model to show that aggregation resulting from spatial variation at two nested scales could greatly increase the likelihood of the coexistence of competing species compared to predictions based on the mean degree of aggregation at a single spatial scale. This result can be explained by Jensen's inequality (Ruel and Ayres 1999; Inouye 2005). Since the coexistence criterion is a nonlinear function of species' distributions, variation in species' distributions at more than one spatial scale has an effect beyond that attributable to only the mean degree of aggregation at a single scale.

In this study I evaluate the role of spatial aggregation in promoting the regional coexistence of competing insects that live in the rotting fruits of a neotropical tree, *Apeiba membranacea*, by parameterizing a model that includes the distribution of competitors across habitat patches at two nested scales. I first estimate the mean density and degree of aggregation for the distributions of the four most abundant specialist species of insect larvae at the scale of each tree, then fit probability distributions to data on variation in mean densities and degrees of aggregation among trees. For three of these species I combine the descriptions of their total aggregation with previous estimates of the strength of their interspecific competition (experiments described in Inouye 1999b). The average densities of these species were fairly constant over a span of 6 years (1993–1998), suggesting that regionally these species can coexist, although the species composition and abundances found under individual trees varied considerably. By combining structured observations of heterogeneity in species' distributions at regional spatial scales with results from competition experiments at a local scale I aim to illustrate an approach for scaling up from studies of interactions in local patchy communities to regional patterns of species coexistence.

Methods

The community of insects inhabiting the fallen fruits of a lowland rainforest canopy tree *A. membranacea* (Tiliaceae) (peine de mico) was studied at La Selva Biological Station in Costa Rica (McDade et al. 1994). At La Selva and in nearby forest fragments *A. membranacea* is found most often in old growth forest and near streams in secondary forest. A wide range of pulp-eating insects colonizes the fruits of *A. membranacea* within hours after they fall from the tree. Nearly 50 insect species were collected inside these fruits, with about ten species found consistently under almost every tree (Inouye 1998). Here I focus on the most abundant of these species: three flies, *Taeneaptera* sp. (Micropezidae), *Richardia* sp. (Richardiidae), and *Chlorops* sp. (Chloropidae), and a small moth, Tineinae sp. (Tineidae). These species appear to be specialists on *Apeiba* fruits. I have no data on competitive interactions between the moth and any other species, but include data on its spatial distribution at the two spatial scales in order to show the generality of the patterns of spatial heterogeneity in this community.

Data on the spatial distributions of all four species were collected in 1996 and 1997. Random samples of 10–36 fruits (mean = 24 in 1996 and 20 in 1997) were collected from underneath 28 (1996) and 22 (1997) trees from May through July. A few trees were sampled twice each season, separated by more than one insect generation, for a total of 30 samples in 1996 and 26 in 1997. Excluding the second sample does not affect the results. Because fruits were collected over a period of 11 weeks, the pattern of aggregation described here represents a mixture of spatial variation and random temporal variation; no temporal trends were identified among or within trees (B.D. Inouye, unpublished data, samples from 1994–1997). Because the model to be parameter-

ized assumes synchronized generations among trees, all variation in larval distributions is assumed to be spatial. Using destructive sampling, all larvae longer than 1 mm in the fruits were identified and counted. Because *A. membranacea* trees at La Selva are widely spaced, each tree can be considered a discrete patch. Thus, the mean density and degree of aggregation among fruits were calculated separately for each insect species for each tree.

Spatial variation at two scales

I used two different measures to quantify the variation in densities among the fruits under a tree. First, I estimated the degree of aggregation of larvae using the crowding index, $J = V/M^2 - (1/M)$, where V is the variance and M is the mean of a species' density (Lloyd 1967; Ives 1988b, 1991). Sevenster (1996) proposed a modification of J that accounts for variation in the size of fruits; Ives' formula assumes that all resource patches are identical. Because the number of larvae per *A. membranacea* fruit was much more variable than pulp volume and not correlated with fruit size, the two methods for calculating J yielded very similar results and the original formula was used for further analysis. Second, negative binomial distributions were used to quantify the degree of aggregation under trees where insect distributions were aggregated, so that this information could be incorporated into the previous model. The crowding index and the negative binomial distribution are related, such that for a negative binomial distribution, $J = 1/k$, where k is the negative binomial's aggregation parameter. Thus more aggregated distributions are indicated by higher values of J, but lower values of k. The crowding index J has greater flexibility and can describe uniform and random distributions as well aggregation ($J \leq 0$).

To test for significant variation in the intraspecific distributions of larvae among trees, I calculated the mean density and the crowding index (J) separately for each tree. Variance in these statistics among trees will arise from sampling error alone, particularly when there is a high variance in density among fruits. To test for variation greater than that expected due to sampling error, I generated null distributions by drawing 3,000 random samples from a negative binomial distribution with the overall mean density and degree of aggregation for each species equal to values calculated from the data pooled over all trees. Samples were equal in size to the field collections. I compared the observed distributions of mean densities and J values to the null distributions with a G-test for goodness of fit (Zar 1999). The relationship between the mean density of a species and its degree of aggregation among trees was investigated using both regressions and Taylor's power law relationship $V = aM^b$ (Taylor 1961; Taylor et al. 1978), where a and b are empirical constants.

In order to parameterize the model describing the regional distribution of individuals as a function of variance at two spatial scales I first used maximum likelihood (Edwards 1992) to fit negative binomial probability distributions to the distributions of larvae in fruits under each tree. The negative binomial parameter k is commonly used to describe the degree of aggregation of individuals among patches (e.g. Atkinson and Shorrocks 1981, 1984; Ives and May 1985; Inouye 1999a), and described data from most trees in this study fairly well. In order to describe variation in the distributions of larvae at the larger (among tree) spatial scale, I used maximum likelihood methods to fit the mean densities and degrees of aggregation with gamma distributions, where the two parameters α and β jointly describe the mean and variance of the distributions (Inouye 1999a). In those few cases where the intraspecific distribution of larvae under a tree tended towards a uniform distribution ($J \leq 0.1$) I arbitrarily assigned $k = 10$, at which point distributions closely resembled a Poisson distribution. Reasonable choices for this value had a very small effect on parameter estimates of the gamma distributions at the regional scale.

Species covariances

To check model assumptions I calculated non-parametric Spearman's rank correlations between the distributions of larvae for every pair of species. Negative correlations between species' distributions of larvae are more likely to reflect resource partitioning than the distributions of emerging adults, which are strongly influenced by interspecific larval competition (Inouye 1999b). At the scale of fruits under a single tree, correlations were based on the number of individuals in each fruit, whereas correlations among trees were calculated using the mean densities of larvae under each tree. P-values for the multiple pairwise correlations were corrected with the Dunn-Sidak method for multiple comparisons for each tree (Sokal and Rohlf 1995). Thus if fewer species were present under a given tree, the α-level for correlations under that tree was higher. This approach corrects only for possible comparisons within each tree, and not for the much larger total number of comparisons across all trees. Individual species densities were also regressed against fruit attributes such as size and condition.

Results

Spatial variation at two scales

The distributions of larvae showed significant intraspecific aggregation among the fruits under individual *Apeiba* trees (Table 1). The amount of aggregation that a species exhibited varied significantly among trees, from highly aggregated to more uniform than a Poisson distribution (Fig. 1). In 1996 all but *Taeneaptera* sp. had distributions of J values that were significantly more

Table 1 The distribution of larvae under most trees is significantly aggregated (χ^2 index of dispersion, Krebs 1999)

	Trees where present (%)	Trees where significantly aggregated (%)	Mean J	Mean density (#/fruit)
1996				
Taeneaptera sp.	100	96	6.38	3.38
Richardia sp.	77	67	6.43	0.74
Chlorops sp.	100	89	3.56	1.29
Tineinae sp.	97	82	5.37	0.91
1997				
Taeneaptera sp.	85	77	3.38	1.29
Richardia sp.	74	78	4.90	0.51
Chlorops sp.	96	96	2.54	2.84
Tineinae sp.	85	77	3.19	0.81

The percentage of trees where larvae of a given species were aggregated and the mean density of each species are based only on trees where a species was present. The mean value of J and the density of larvae per fruit are weighted means based on the number of fruit sampled per tree

variable than the null distributions based on sampling error ($P < 0.01$). In 1997 all four focal species had distributions of J values that were significantly more variable than expected (all $P < 0.05$). The mean density of a species under different trees also varied more than 20-fold (Fig. 2). In both years all species had distributions of mean densities that were significantly different from their null distributions based on sampling error (all P-values < 0.01). Maximum likelihood estimates of parameters for the gamma distributions fit to the mean densities and degrees of aggregation are shown in Table 2. The mean of the gamma distribution is α/β, but the mean to variance ratio is determined solely by β,

Fig. 1 Distributions of the crowding index, J, per tree for the four focal taxa in 1997. **a** *Taeneaptera*, **b** *Richardia*, **c** *Chlorops*, **d** Tineinae

with values of β less than one indicating more variable (right-skewed) distributions.

For all species, the aggregation of larvae under a tree varied independently of the mean density under trees. There were no significant correlations between the mean density of larvae and J in either year (all P-values > 0.19). As another indication that the mean densities and degrees of aggregation were not related, estimates of the slopes of Taylor's power law were not significantly different from expectations given a null hypothesis of constant negative binomial parameter k (all P-values > 0.10).

Larval aggregation due to egg-laying in clutches may also affect coexistence, if the superior competitor lays larger clutches (Heard and Remer 1997). Using least-squares maximum likelihood to fit the model in Jaenike and James (1991), average clutch sizes of the four species in this paper are all estimated to be near one (results not shown). Sevenster (1996) has criticized the use of this method for estimating clutch size when J is density dependent, but for the species in this study the degree of aggregation was density independent.

Species covariances

At the scale of fruits under a single tree, distributions of larvae of the four focal species were significantly correlated in less than 4% (7/181) of possible pairwise correlations in 1996 and 1% (1/91) pairwise correlations in 1997 ($\alpha = 0.05$ *per tree*), which is less than the expected number of significant correlations given the number of trees sampled. Including data on additional species (311 additional pairwise correlations) revealed no new significant associations (B.D. Inouye, unpublished data). Thus, the most common insect species in *A. membranacea* fruits are independently distributed among fruits under a tree. At the spatial scale of trees, none of the pairwise correlations among the mean densities of the four focal species were significant ($\alpha = 0.05$) in either year. Fruit size and condition were never significant predictors of larval distributions.

Scaling up to predict regional coexistence

Here, I combine data on the patterns of aggregation described in the previous section with data on interspecific competition, which allows me to parameterize an existing model for the effect of aggregation at two spatial scales on coexistence (Inouye 1999a). The model described in Inouye (1999a) is based on the Hassell and Comins (1976) competition equations, but is expanded to include independent probability distributions of competitors among discrete patches. This allows calculation of a boundary between regions of competitive exclusion and coexistence, which depends on both the strength of competition and degree of aggregation of the superior competitor. Thus, the only parameters that are
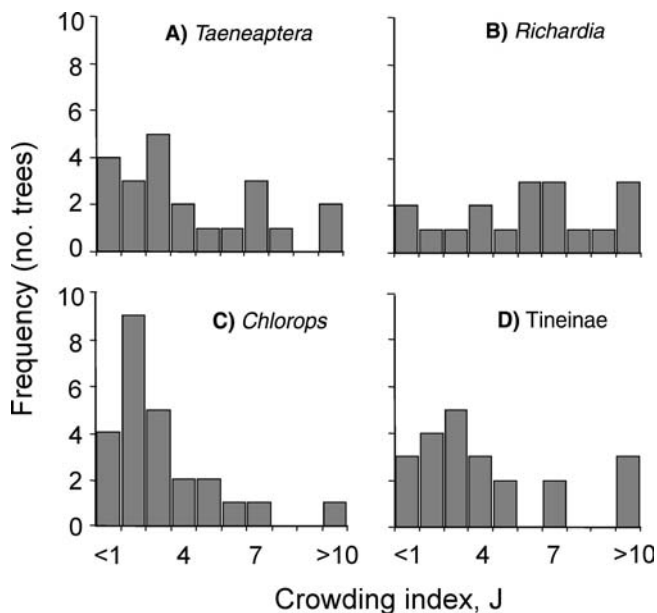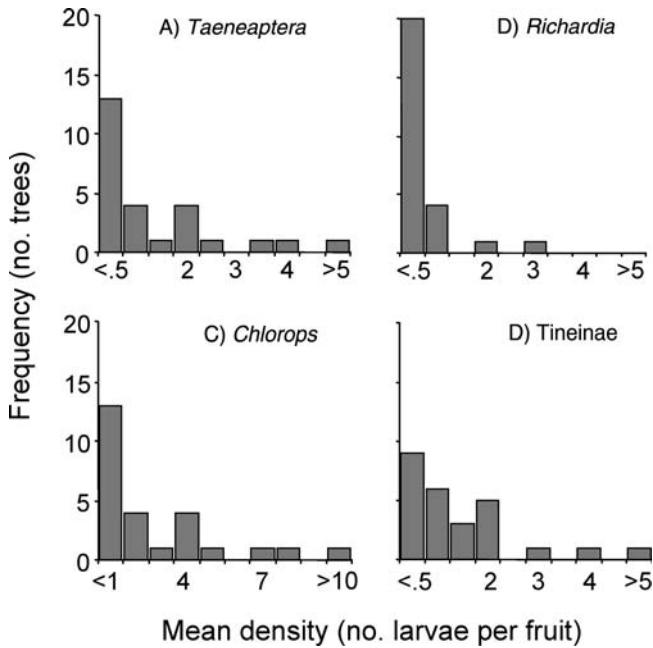
Fig. 2 Distributions of the mean density of insect larvae per tree for the four focal taxa in 1997. The mean densities are weighted by the number of fruits sampled per tree. **a** *Taeneaptera*, **b** *Richardia*, **c** *Chlorops*, **d** Tineinae. Note that a different scale is used for **c** *Chlorops*

Fig. 3 Coexistence criterion assuming variation at a single spatial scale for three insect species. The *curve* shows the maximum competition coefficient allowing the coexistence of an inferior competitor versus the degree of aggregation of the superior competitor. The generic initial of the superior competitor in each species pair is listed first; T = *Taeneaptera* sp., R = *Richardia* sp., and C = *Chlorops* sp. The *vertical bars* show 95% confidence intervals for the competition coefficients; *horizontal bars* show the region containing 95% of the variation of the best-fit gamma distributions for the degree of aggregation (Table 2)

required to fit this model are those describing probability distributions of competitors among patches and the competition coefficients. Inouye (1999b) reported the results of pairwise competition experiments among three species: *Taeneaptera* sp., *Richardia* sp., and *Chlorops* sp. For each of the species pairs, one species was clearly the superior competitor, providing a competitive ranking of *Taeneaptera* sp. superior to *Richardia* sp., and both *Taeneaptera* sp. and *Richardia* sp. superior to *Chlorops* sp. For all three species-pairs the effect of the inferior competitor on the superior competitor was not significantly different from zero. Thus, along with their spatial distributions, only the competition coefficients describing the effect of the superior competitor on the inferior competitor determine the coexistence criteria (see also
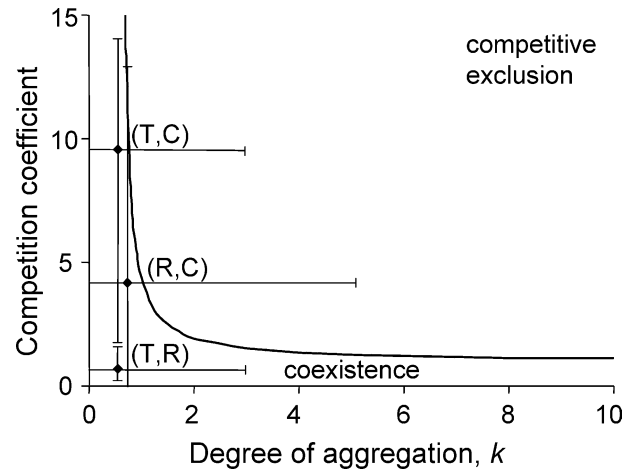
Ives 1988b; Tilman 1994). The competition coefficient estimates are based on fitting the Hassell and Comins (1976) competition equations to experimental data, which are the same equations used to describe competition in the model (Inouye 1999a).

The effects of spatial variation in competitor density at a single spatial scale on coexistence are shown in Fig. 3. The curve that separates the region of competitive exclusion from the region of coexistence shows the dependence of coexistence on both the degree of aggregation and the competition coefficient of the superior competitor. The location of this curve was calculated assuming that the single species carrying capacities for each species are equal; this result is robust to deviations of this assumption by at least an order of magnitude (Inouye 1999a). The carrying capacities for these species are estimated to differ by only a factor of approximately

Table 2 Maximum likelihood estimates of parameters for gamma distributions (α, β)

Species	α	β	α/β	α	β	α/β
	Distribution of means 1996			1997		
Taeneaptera sp.	1.41	0.46	3.07	0.50	0.35	1.43
Richardia sp.	1.39	2.04	0.68	0.83	1.44	0.58
Chlorops sp.	1.97	1.71	1.15	1.68	0.48	3.50
Tineinae sp.	1.92	2.11	0.91	1.23	0.89	1.48
	Distribution of k values 1996			1997		
Taeneaptera sp.	1.9	7.55	0.25	0.43	0.78	0.55
Richardia sp.	0.13	0.35	0.37	0.25	0.34	0.74
Chlorops sp.	0.36	0.51	0.71	0.29	0.31	0.94
Tineinae sp.	0.29	0.59	0.49	0.62	0.93	0.67

In order to describe variation among trees in the degree of aggregation and mean density of larvae, gamma distributions were fit to both variables. The degree of aggregation for each tree was measured as the maximum likelihood value of the aggregation parameter k from a negative binomial distribution

two (B.D. Inouye, unpublished data). The three points on Fig. 3 show the 1996 maximum likelihood parameter estimates for the superior competitor of the three pairs of species for which both aggregation and the strength of competition were measured. Since the curve was calculated assuming only one spatial scale of variation (i.e. all trees have the same mean density and degree of aggregation), the points show the mean degree of aggregation for each pair. Note that *Richardia* sp. is shown as both an inferior and a superior competitor depending on the pair.

The vertical bars for the points in Figs. 3 and 4 represent uncertainty in the estimates of the effective competition coefficients, while the horizontal bars indicate the range of variation in aggregation. The vertical error bars for the three species-pairs show the 95% confidence intervals of the MLE of the competition coefficients. The horizontal bars in Fig. 3 show the region containing 95% of the gamma distributions that were fit to the degree of aggregation of the superior competitors (*Taeneaptera* sp. and *Richardia* sp.). The minimum regions containing 95% of the probability for the gamma distributions were calculated based on the MLE parameter estimates (α and β in Table 2). Because the gamma distributions are highly skewed, these quantiles are not symmetric. The points and bars shown for the degree of aggregation in Figs. 3 and 4 are for the data from 1996; bars for 1997 data would be smaller because the average degree of aggregation for all species was slightly higher and less variable.

The competition coefficient estimates for two of the species-pairs are greater than one, which implies that aggregation (or some other coexistence mechanism) is necessary for the persistence of *Chlorops* sp. The fact that the points for all three species pairs fall below the curve, in the region where coexistence is predicted, means that aggregation at a single spatial scale is on average sufficient to allow the coexistence of these competitors. However, because of variation in the degree of aggregation, aggregation under many individual trees was not sufficient to allow coexistence. In order to assess the full role of aggregation in promoting the regional coexistence of these competitors, it is necessary to include the effects of variation at both of the spatial scales. Although there is also significant spatial variation in the mean densities of the focal species among trees (Table 2), this variation is not shown on these axes.

Figure 4 is similar to Fig. 3, except the interpretation of the horizontal axis has been changed slightly. Rather than the mean degree of aggregation, this axis now represents the total amount of aggregation when both spatial scales are considered. There are now two curves separating regions of competitive exclusion and coexistence, as there are two species of superior competitors among these three pairs. The locations of these curves are calculated using the regional gamma distributions of both mean densities and degrees of aggregation
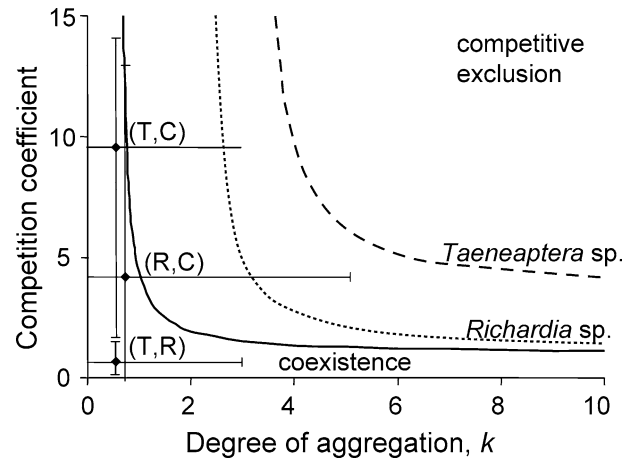

Fig. 4 Coexistence criterion using variation at two nested spatial scales for three insect species. See text for alternative interpretation of the *x*-axis. All *labels* and *bars* as for Fig. 3. The *two dashed curves* reflect the additional effects of variation among trees in the distributions of the superior competitors, *Taeneaptera* sp. and *Richardia* sp. The *curve* labeled for *Taeneaptera* sp. applies to both species pairs where *Taeneaptera* sp. is the superior competitor

(Table 2) for the superior competitors, *Taeneaptera* sp. and *Richardia* sp., in 1996. In order to calculate the position of these curves, the best-fit parameters for the gamma distributions were used to parameterize the model from Inouye (1999a). These curves take into account the separate effects of both of kinds of variation on the potential for coexistence. A comparison of Figs. 3 and 4 clearly shows that regional spatial variation among trees can greatly contribute to the coexistence of these competing insect species. The curves that include the effects of variation among trees place the points for the three species pairs much further inside the region of coexistence.

Discussion

Aggregation among fruits and variation among trees

The insects that feed on the pulp of *A. membranacea* fruits all have distributions among fruits that reflect strong intraspecific aggregation. Previous models have demonstrated that such aggregation promotes the coexistence of competitors, and that the degree of aggregation necessary for coexistence depends on the strength of competitive interactions (Atkinson and Shorrocks 1984; Ives and May 1985). Furthermore, variation at multiple spatial scales can contribute to the regional distribution of competitors. The results of this study show that the total variation in the density of these insects depends on variation at two spatial scales, and not just aggregation at a single scale. By parameterizing a model of the effect of aggregation on coexistence I found that spatial variation alone is sufficient to explain the coexistence of a set of competing species, despite strong competition within patches.

Interspecific competition among the three fly species is strong enough that aggregation, or another coexistence mechanism, is necessary for their coexistence (although *Taeneaptera* sp. and *Richardia* sp. might coexist without spatial variation, depending on the balance of their carrying capacities). The effect of the mean degree of aggregation at a single spatial scale is sufficient for promoting the coexistence of these species (Fig. 3). However, the degree of aggregation varies greatly among trees, so that if each tree were an independent community these three species pairs would not be predicted to coexist under every tree (note the horizontal bars showing the 95% quantiles for the degree of aggregation in Fig. 3). Annual variation in the mean degree of aggregation (cf. Table 2) may also be sufficient to move the points for some species into the region of competitive exclusion. As long there is some movement among trees (i.e. they are not independent communities), when spatial variation among trees is included in calculating the distribution of the superior competitors the effect of aggregation on coexistence is greatly enhanced. In Fig. 4 the region of coexistence incorporating variation at both spatial scales is larger than the region of coexistence based on a single spatial scale. The effect of regional variation among trees in both mean densities and degrees of aggregation is sufficient that these competitors are predicted to coexist regionally and under all individual trees.

The model that was used to scale up to regional coexistence includes several important assumptions about the probability distributions describing species' larval distributions among fruits and trees (Inouye 1999a). Two assumptions about the statistical independence of species' distributions were closely met. The first is that the competitors have independent (uncorrelated) distributions at each scale. This was evaluated by testing correlations among species-pairs at the scales of fruits and trees. Ovipositing females of the species in this study appear to use both trees and fruits independently of other species. Violations of this assumption about the independence of species' distributions would require use of a different model that included terms for species covariances. The second assumption, that at the larger spatial scale the mean densities and degrees of aggregation are independent, was also supported by the data. A third assumption is that the distributions of mean densities and degrees of aggregation remain static long enough to reach a regional equilibrium, an assumption that is likely to be violated. Thus, the results shown in Fig. 4 serve more to illustrate the important consequences of including variation at multiple scales, the sufficiency of spatial variance for promoting coexistence among these species, and the use of regional observational data for scaling up predictions from local-scale experiments, than for making detailed quantitative predictions.

The diverse coexistence mechanisms that have been proposed for species in patchy and ephemeral habitats are not mutually exclusive (e.g. Ives 1988a). Despite the sufficiency of spatial variation in density at two scales for promoting the coexistence of *Apeiba*-feeding insects, additional coexistence mechanisms may affect this community and moderate competitive interactions. Previous studies in patchy and ephemeral habitats suggest that resource partitioning does not play an important role in allowing coexistence in these communities (Rosewell et al. 1990; Shorrocks and Sevenster 1995; Sevenster and van Alphen 1996; Wertheim et al. 2000; Krijger 2000). There was also little evidence to suggest that classical resource partitioning at the spatial scales of trees, fruits, or even within fruits (B.D. Inouye, personal observations) is important for mediating the interactions among these *Apeiba* pulp-feeding insect species. The fly species whose coexistence was modeled in this study all colonize fruits at the same early stage and broadly overlap in the time they spend in the fruits. However, as the *A. membranacea* fruits became substantially decayed I found many species that were never observed inside recently fallen fruits. Temporal resource partitioning does occur for some species in the larger *Apeiba*-feeding community, and has been found to be important in other studies of insects in patchy and ephemeral habitats, including rotting fruits (Colwell 1969). Finally, logistical constraints allowed estimation of only pairwise interactions in the competition experiments (Inouye 1999b), even though it was common to find more than two species of larvae sharing an *A. membranacea* fruit. Higher-order interactions when more than two species are present (Adler and Morris 1994; Worthen and Moore 1991) could also affect the outcome of larval competition and thus affect regional coexistence criteria, but these coexistence criteria would still depend on species' distributions among patches.

Conclusions

In the decades since the aggregation mechanism of coexistence was proposed (Atkinson and Shorrocks 1981; Hanski 1981), many studies have documented that insects using patchy and ephemeral resources can have highly aggregated distributions (e.g. Rosewell et al. 1990; Grimaldi and Jaenike 1984; Sevenster 1996; Wertheim et al. 2000; Krijger and Sevenster 2001), but few studies have included data on the strength of competition. In addition to demonstrating the presence of aggregation among the fruits under a single *A. membranacea* tree, I found significant regional variation among trees in mean densities and degrees of aggregation for the larvae of four species of insects. I used summaries of these regional observational data, along with results from local-scale experiments, to parameterize a mathematical model to yield predictions about the regional outcome of species interactions. This approach is different from previous studies of aggregation not only because it explicitly included nested spatial scales, but also because experimental estimates of competition coefficients were available, allowing me to fully

parameterize a regional coexistence model. I found that aggregation at one spatial scale (among fruits) and variation at a larger spatial scale (among trees) were together sufficient to explain the coexistence of competitors feeding on *A. membranacea* fruits. These results suggest that since regional spatial variance may depend on processes at multiple spatial scales, the aggregation mechanism of coexistence may be more widely applicable than previously appreciated.

Variation at multiple spatial scales may influence ecological and evolutionary processes in addition to competition and coexistence. For example, other species interactions (besides competition), patterns of selection, and mating can also be determined at local scales, and yet vary regionally. Whenever the effects of spatial heterogeneity are nonlinear, including variation at multiple scales is one key to scaling results from detailed data at smaller scales up to conclusions at larger spatial scales. The results of models that include measures of spatial variances and covariances can be qualitatively different from predictions based on mean values at a single spatial scale. This study illustrates a case where estimates of spatial heterogeneity at two nested scales were combined with experimental data from the smallest, most simply manipulated spatial scale. Hopefully this approach will allow more rapid progress towards linking empirical and theoretical studies and improve our ability to make regional inferences from local experiments.

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