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INFERRING COLONIZATION PROCESSES FROM POPULATION DYNAMICS IN SPATIALLY STRUCTURED PREDATOR–PREY SYSTEMS

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Abstract. We examine how spatial subdivision of predator–prey systems affects colonization processes in metapopulations. Dynamics of the herbivorous spider mite *Tetranychus urticae* (prey) and the predatory mite *Phytoseiulus persimilis* are highly unstable on isolated bean plants (*Phaseolus lunatus*) and ultimately result in extinction of prey and predators. Assembling a collection of 90 plants without any dispersal barriers (a super-island experiment) does not modify the persistence of the predator–prey system. Subdividing the system into a metapopulation with barriers for dispersal (a collection of eight islands with 10 plants per island) leads to persistence of the predator–prey dynamics for many generations. In this paper, we use the time series of colonization events and prey and predator densities from the super-island and metapopulation experiments to understand how colonization processes of prey and predatory mites are altered by spatial subdivision. Using survival analysis, we estimate how prey and predator colonization probability is affected by densities of the colonist pool at different distances from the target plant. Contrasting the results from the super-island and metapopulation experiments reveals that spatial subdivision affects the discovery rate of prey outbreaks by predatory mites and differentially affects colonization by prey and predators. Prey colonization is primarily determined by local densities of prey in spatially subdivided systems, whereas predator colonization retains primarily ''global'' influences. Our analysis of colonization processes suggests mechanisms accounting for stability in the metapopulation experiments and provides the quantitative basis for the development of colonization functions to explore these mechanisms in predator–prey models of acarine systems.

Key words: colonization; logistic regression; metapopulation; Phytoseiulus persimilis; *predator–prey dynamics; spatial subdivision; survival analysis;* Tetranychus urticae.

INTRODUCTION

Theory suggests predator–prey interactions have an inherent propensity to be unstable, yet real predator–prey systems persist, and many are apparently dynamically stable. Spatial processes, and especially metapopulation dynamics, constitute one class of possible explanations for this apparent contradiction. In the simplest metapopulation models, local populations go extinct but the collection of populations persists because patches are recolonized by immigrants from extant populations (e.g., Levins 1969, 1970, Reddingius and den Boer 1970, Levin 1976, Crowley 1981, Hanski and Gilpin 1997).

Experimental populations of prey and predatory

mites appear to exemplify such dynamics (e.g., Huffaker 1958, Nachmann 1981, 1991, van de Klashorst et al. 1992). Janssen et al. (1997*a*) conducted a series of experiments designed to understand the mechanisms causing persistence. The dynamics of the herbivorous spider mite *Tetranychus urticae* and the predatory mite *Phytoseiulus persimilis* on single bean plants (*Phaseolus lunatus*) were highly unstable (Janssen and Sabelis 1992, Pels and Sabelis 1999). Prey (i.e., the herbivorous mites) were driven extinct rapidly by predators and then predators declined to extinction. A collection of plants (Fig. 1) that allowed for unrestricted migration of prey and predators did not promote stability: prey populations in a system with 90 plants persisted longer than single plant systems, but the eventual result was the elimination of prey by predators. It was only when the system was subdivided into a series of connected islands with restricted dispersal between is-
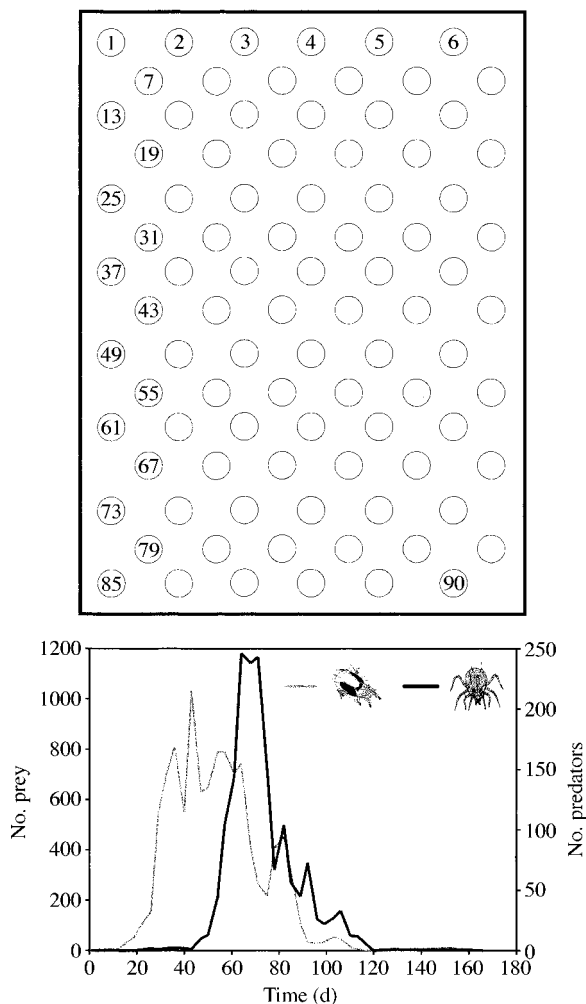
FIG. 1. Spatial arrangement of plants and numbering system for sites (top panel) for the super-island experiment. Fluctuations in total density of prey (thin line) and predatory (thick line) mites on the super island (bottom panel).

lands (Fig. 2) that long-term persistence was achieved. The metapopulation system, presented in Fig. 2, exhibited persisting predator and prey populations for >390 d which represents >30 generations.

Our major goal is to explain how the spatial subdivision of this predator–prey system promotes persistence. Clearly subdivision is crucial, but how has it modified population processes? Long-term persistence of a population over many generations requires density-dependence to be operating at a global level of the spatially subdivided system (e.g., Royama 1992, Murdoch 1994). It is difficult to summarize briefly all of the possible ways that this introduction of spatial subdivision could affect persistence or stability. Any broad classification is subject to criticism, but we can categorize explanations on how stability arises in spatially structured predator–prey systems into two major classes by considering how they act to modify stability.

Stability can occur via mechanisms that generate new density dependence which appears either at the level of the patch or larger scales. Examples include creation of a spatial refuge with entry-exit dynamics (e.g., McNair 1986, 1987, Sabelis et al. 1991, Abrams and Walters 1996), changes to the predator functional response on a global scale (e.g., Murdoch and Oaten 1975), or creation of density-dependent immigration (e.g., Nachman 1991, Murdoch et al. 1992, Nisbet et al. 1992). Alternatively, there are mechanisms that modify the strength of existing density-dependence. Examples include reducing the effective search rate of predators leading to reduced amplitude fluctuations (e.g., McCauley et al. 1993, McCauley et al. 1996, de Roos et al. 1998) or reducing the effective growth rate of prey (e.g., Nisbet et al. 1997). The generation of asynchrony among groups of patches or spatial heterogeneity is crucial for both mechanisms (e.g., Reeve 1988, de Roos et al. 1991, Taylor 1991, Ives 1992, Adler 1993).

Since the sequence of events on a colonized plant is not altered by spatial subdivision (i.e., both prey and predators overexploit their respective resource causing its extinction on both the superisland and metapopulation), the key to understanding which mechanism(s) increase(s) the persistence observed in the metapopulations is to determine how colonization processes for prey and predator have been modified between the super-island and the metapopulation experiments. That is, we need to evaluate changes in the relative contribution of local and global dispersal/movement by prey and predators that occurred with spatial subdivision. Ideally, we could collect data on the movement of individuals on both the super-island and metapopulation, along with experiments that manipulate prey and predator densities to measure how probability of colonization is affected at different distances from the perturbation; but such experiments were not done. Indeed, these data are rarely available in lab or field situations. Following known individuals for long enough in the context of a population experiment to measure movement is impracticable in most systems (Harrison 1989, Delestrade et al. 1996, Kuussaari et al. 1996, Doncaster et al. 1997, Turchin 1998), and experiments to perturb local densities and measure changes in the colonization probability elsewhere are daunting. In the absence of quantitative observations on movement patterns of individual prey or predators in the population context of the experiment, the challenge is to infer from population-level data the changes in individual movement and colonization that occur following spatial subdivision. We can then explore how these changes affect mechanism(s) promoting persistence in the metapopulation runs.

We use here the time series of colonization events along with corresponding observations of the temporal and spatial dynamics of prey and predatory mites to infer the factors affecting local colonization. To pro-
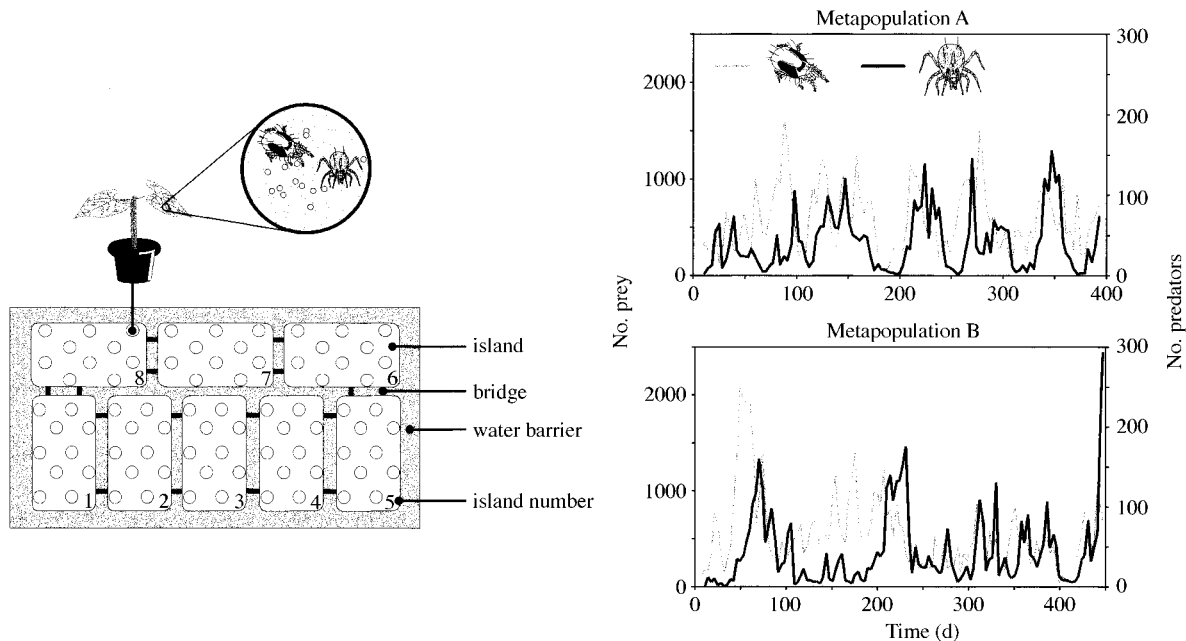
FIG. 2. Spatial configuration of eight islands and bridges for the metapopulation experiments (left panel). Plants on each island are numbered beginning with the plant in the lower left-hand corner of the island and progressing across a row. The right panels show the temporal dynamics of prey (thin line) and predatory (thick line) mites in the entire metapopulation for the two experimental systems (A and B).

vide insight into the source of the stability in the metapopulation runs, we contrast results from the two spatial configurations (i.e., the superisland and metapopulation) on whether colonization occurs via local dispersal from nearby plants or involves more global movements of individuals among distant islands. Colonization events (e.g., the transition from prey absent to prey present on a plant at a particular point in time is an event) can be assembled from the record of mites on individual plants, along with knowledge of the plant replacement schedule. We analyze these events by looking for patterns in the relationship between colonization probability and system states. We measure the conditional dependencies of colonization for prey and predators on past or present system states and determine the spatial extent of these dependencies, using survival analysis. With this information, we can draw conclusions about the relative contribution of local and global dispersal for prey and predators, and suggest which of the mechanisms altering persistence should be investigated further. In addition, these analyses provide the benchmark relationships needed to construct theoretical models of the colonization process that could be used in the context of a metapopulation predator–prey model to investigate stabilizing mechanisms. A supplementary goal is to show how the analysis of time series may be used to study colonization processes in other laboratory or field systems where similar data exist (e.g., Holyoak and Lawler 1996).

This is essentially a correlation analysis and is fraught with the usual interpretation difficulties (i.e.,

correlations among putative causal variables, etc.), but the hope is that the results may constrain the range of plausible processes. For example, a strong effect of the density of mites on neighboring plants is unlikely to have been generated by system-wide mixing of the colonist pool. In addition, we can assess the biological plausibility of our empirical models by comparing the direction of effects of prey and predator densities on colonization in the population context with results from independent behavioral experiments (Sabelis and van de Baan 1983, Sabelis et al. 1984, Sabelis and Dicke 1985, Sabelis and van der Weel 1990, Janssen et al. 1997b, Margoles et al. 1997, Janssen 1999, Pels and Sabelis 1999). These experiments suggest how dispersal of prey might be related to fluctuations of prey density on isolated plants (i.e., prey appear to disperse only when food is exhausted) and how predators may locate high local densities of prey. Can we detect the expression of these behavioral mechanisms in the population-level experiments?

Our primary interest is the contrast between the super-island experiment and the metapopulations. However, there were quantitative differences between the metapopulation runs. Despite the fact that these replicate metapopulation runs (system A and B) were set up under identical conditions using comparable biological material, there were marked differences in the predator–prey fluctuations and the cyclicity of the time-series (Janssen et al. 1997a). Thus, we also investigate whether there are detectable differences in the colonization process between the metapopulation runs.

In this paper, we address four major questions using the time series of colonization events and the dynamics of prey and predatory mites on plants. (1) What are the factors controlling colonization and how do they vary with spatial subdivision? (2) What is the relative importance of local versus global dispersal for both prey and predators? (3) Can we detect patterns at the population level that are expected from short-term behavioral experiments? (4) Are there major differences in factors affecting colonization events between the replicate metapopulation runs that could account for the quantitative differences in their dynamics?

METHODS

Janssen et al. (1997*a*) present the detailed methodology for the super-island and metapopulation experiments. Here, we provide a general description, stressing features associated with colonization, and methods of analysis of colonization probability from observations on the dynamics of prey and predatory mites.

The super-island experiment consists of 90 plants arranged in a rectangular array (Fig. 1); pots were imbedded in a single styrofoam island that floated in a tray of water. The experiment began by inoculating the system with six adult female spider mites over a one-month period to introduce temporal asynchrony into the system, followed by the addition of 18 adult predatory mites on clean plants. The location and date of the inoculation were noted, and these colonization events were not included in our analyses. The abundance of adult prey and adult predatory mites was observed on each plant twice weekly for 155 d. Care was taken to standardize the plant state for colonization and exploitation by prey mites. Once a plant was overexploited by mites and it was determined that all mites had left the plant (three consecutive sampling dates with zero mites), the plant was replaced with a one-week-old plant pruned to two leaves. When the quality of an uninfested plant declined, as judged by its appearance, it was replaced with new one-week-old plants to maintain plant quality. The metapopulation experiments subdivided the single styrofoam island into eight styrofoam islands (10 plants per island for 80 plants in total) connected by cork bridges (Fig. 2), with the space for 10 plants being lost in the process. Two replicate systems (referred to below as system A and B, or run A and B) were housed in the same environmental chamber, and the initial conditions for inoculation of mites were identical (prey inoculated on three islands, predators on one island). Plants were kept pruned so that there were no direct connections among them, and aerial dispersal was not possible because there were no breezes in the growth chamber. Thus, the mites could disperse only by walking down the plant; crossing the damp soil, styrofoam, and maybe bridges; and climbing up another plant. The bridges were below the rims of the styrofoam islands, making them difficult for the mites to discover and thereby reducing the interisland dispersal rate.

To estimate the various colonist pools at different distances from target plants on the superisland, we assigned plants to one of three categories. Nearest-neighbor plants are directly beside the target plant (one-step dispersal), next-nearest neighbors include plants that can be reached with one additional step from neighboring plants (two-step dispersal), next-next-nearest neighbors require an additional step (three-step dispersal), and non-neighborhood plants are the remaining plants. Given the shape of the array, the number of neighbors, next-nearest neighbors and non-neighbors varies considerably among plants. For example, plant 5 located on an edge has four nearest neighbors and six next-nearest neighbors, while plant 40 near the center has six nearest neighbors and 12 next-nearest neighbors. Because we wish to draw comparisons over different distances and among experiments, the number of potential colonists for a target plant at each sampling date was determined by averaging over the actual number of plants in each category. In the metapopulation experiment, we only considered the distinction between nearest-neighbors and non-nearest neighbors on an island because of the small number of plants remaining after considering nearest neighbors and the geometry of the systems. The number of nearest neighbors differed for plants on the island and the exact number was used in the calculation of potential colonists for each target plant. A brief description of the independent variables used in the analysis is presented in Table 1. Observations from exploitation of single plants by prey mites in the absence of predators (Janssen and Sabelis 1992, Pels and Sabelis 1999) suggest that prey only disperse from plants once the majority of plant material has been consumed (i.e., at the end of a prey only episode). Thus, we included in our list of candidate independent variables, estimates of the rate of decline of prey population at different spatial scales (i.e., rate of decline of prey on nearest neighbor plants, island level, etc.). Analogous arguments may apply for the detection of prey-occupied plants by predators, or predator avoidance and we also use the relevant rates of change that pertain to these processes in our models. To test for the effect of plant quality (e.g., Takabayashi et al. 1994), the age of a plant was also included in the analysis.

Using the information on the time series of mites on each plant and the detailed replacement schedule for plants (which includes information on refractory periods to determine accurately the number of plants unavailable for colonization), we can estimate the probability of colonization (i.e., the colonization frequency) at time t from the number of plants changing state from uninhabited and available for colonization, to inhabited by adult mites. Note that juveniles were not sampled so the transition to the colonized state is based on the appearance of adults. However, juvenile dispersal oc-

TABLE 1. Regression variables defined for prey.

Variable name	Definition
Prey density on neighboring plants	(Sum of densities on nearest neighbors)/(number of nearest neighbor sites)†
Local prey density	(Sum of prey densities on target plant and nearest neighbors)/(number of plants)
Island prey density	(Sum of prey on plants except for target plant)/9
Prey density on adjacent islands	(Prey density on nearest-neighbor islands per plant)/(number of adjacent islands)
Rate of change of prey density	[Sum of (prey density at time t − prey density at time t − 1)]/(corresponding number of plants)‡
Plant age at colonization	Plant age at colonization
Date	Day of colonization (time in days since start of experiment)

Notes: Predator variables were calculated following the same equations where appropriate. The variables were then lagged in time. Only two time lags are appropriate, given the life history and timing of development of prey and predatory mites. Variables were also indexed according to spatial proximity (i.e., adjacent islands, islands bordering adjacent islands, etc.).

† Plants on islands have differing numbers of nearest-neighbor plants. The exact number of nearest neighbors for each plant on each island was used. For the analysis of the super-island experiment, nearest neighbors, next-nearest neighbors, and next-next-nearest neighbors were defined for each target plant.

‡ We only considered negative rates. All positive rates were set to zero in the analysis.

curred rarely in these experiments. Infested plants were not replaced until all mites had left the plant (the refractory period); plants had to be free of adult prey for two weeks and free of adult predators for 1.5 wk, thus ensuring that all immatures had sufficient time to develop or disperse. Logistic splines (S-PLUS 1997) were used to describe the temporal trends in colonization probability for prey and predators on islands, the metapopulation, and the superisland.

The series of observations of whether a plant is colonized (1) or uncolonized (0) is a binary time series. Our general approach is to use survival analysis, treating the times to colonization as the independent observations, but modeling the probability of colonization over any sampling interval (the hazard function) as a logistic function of the covariates. This enables us to write down a likelihood, which enables our model to be fitted by logistic regression (Hosmer and Lemeshow 1989), and further allows some (but not all) inference to be performed exactly as if our model really were a logistic regression model. Hosmer and Lemeshow (1999) discuss fitting hazard models using binary regression techniques.

For each colonization event it is possible to deter-

mine how many sampling intervals it took for the plant to become colonized. Let this be T_j for the jth colonization event. We then modeled the probability of colonization per sampling interval h as a logistic function of the vector of covariates **x**:

$$h(\mathbf{x}) = \frac{\exp\left(\beta_0 + \sum \beta_i x_i\right)}{1 + \exp\left(\beta_0 + \sum \beta_i x_i\right)}$$

Since the covariates change with plant and time, h will not be constant over the entire waiting time to a colonization, but under the mild assumption that h can be treated as constant over each sampling interval, it is possible to write down the probability of observing a particular wait, T_j. Let $\{\mathbf{x}_1^{[j]}, \mathbf{x}_2^{[j]} \ldots \mathbf{x}_{T_j}^{[j]}\}$ be the vectors of covariates for the plant on which the jth event happened for each sample time leading up to the jth event. Then the probability of T_j under the model is

$$P[T_j] = h(\mathbf{x}_{T_j}) \prod_{i=1}^{T_{j-1}} [1 - h(\mathbf{x}_i)].$$

This probability is implicitly a function of the model parameters β, and hence the likelihood for β can be written as follows

$$L(\beta) = \prod_{i=1}^{n} P[T_i]$$

where n is the number of colonization events. This likelihood is exactly the same as we would have obtained by (wrongly) treating each observation of whether or not a plant had been colonized as an independent observation of a Bernouilli trial with probability of success given by $h(\mathbf{x})$. This is the model underlying logistic regression. Hence, our likelihood can be maximized using any package that can perform logistic regression. All logistic regression analyses were performed using SAS (1998), and model selection was based on comparisons using stepwise and backward selection techniques (selection criterion for variable entry or removal is $P < 0.05$). We initially include 21 covariates as candidates in the model and, as always with statistical model selection, the reader should bear this in mind when interpreting P values associated with selected model terms (Sokal and Rohlf 1995). Similarly, there is always the possibility that one or more of the covariates included in our model are spurious. One way of reducing this likelihood is to compare models obtained from both stepwise variable selection (i.e., forward selection and re-evaluation of significance of previously entered variables with each addition) and backward selection techniques (all variables initially entered, and variables removed following partial F tests). However, the fact that there are two independent runs of the metapopulation experiments allows us to compare the models obtained for each run separately and compare the independent variables chosen from the separate analysis.

It is important to notice that, while our model can be fitted by logistic regression, not all of its statistical properties are those of a logistic regression model. In particular, a standard logistic regression model treats all observations of ones (colonized) and zeros (uncolonized) as being observations of independent random variables, so that every zero and every one contributes one degree of freedom to the analysis. This independence assumption is invalid in the current context: our independent observations are really times to colonization (expressed as number of sample intervals it took to get colonized), the total degrees of freedom is hence *n,* the number of colonization events: a number that is very much smaller than the total number of zeros and ones in a data set.

In practical terms the total degrees of freedom are important in determining the absolute goodness-of-fit of the model. The deviance of the model should be distributed as χ^2_{n-p} (where p is the number of model parameters) if the model is a good fit. Under the incorrect logistic regression model, the degrees of freedom for this χ^2 would be much higher.

When comparing the two nested models to test the significance of model terms, it is the difference in deviance between the two models that matters. If the models are equally good (or even bad) then the difference in their deviances should be distributed as Π^2_{p1-p2}, where p_1 is the number of model parameters of the more complicated model, and p_2 is the number of parameters in the reduced model. Notice that the total degrees of freedom do not feature in this result, so that model selection based on deviance differences is unaffected by the total degrees of freedom in the data. In practice this means that model selection for our approach can be performed using standard logistic regression packages. Finally, it is possible to show using distributional results for generalized linear models, that the standard asymptotic confidence intervals for parameters estimated by logistic regression will be unaltered when using our model.

Results

Analysis of super-island experiment

Fig. 1 shows the temporal dynamics of prey and predatory mites on the superisland. Prey densities increase over the first 30 d, fluctuate around relatively high levels for the next 30 d, decrease because of predators, recover slightly, and then ultimately collapse to extinction. Fluctuations in prey colonization probability (i.e., the number of colonization events per number of available plants) show a similar trajectory (Fig. 3a), including peaks at approximately day 45 and day 80. These peaks coincide with high levels of total prey density. At the first peak, ~15% of the available plants are colonized and the percentage is reduced to only 3% in the second maximum. Predator colonization (Fig.
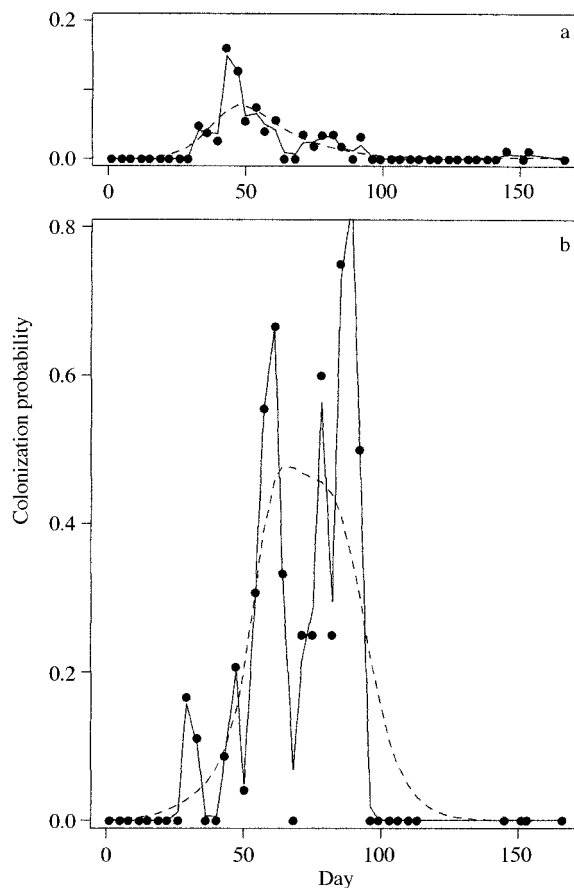

FIG. 3. Colonization probability of (a) prey and (b) predators over time in the super-island experiment. The temporal trends are highlighted using splines with three degrees of freedom (for long-term trends; dashed line) and 20 degrees of freedom (for short-term trends; solid line).

3b) increases to an initial peak of 65% at day 65 followed by a second roughly three weeks later.

Prey colonization on target plants depends on both local (i.e., neighborhood) and global (non-neighborhood) prey variables (Table 2). The model explains a significant amount of variation in the probability of colonization as indicated by the χ^2 statistic ($P < 0.0001$) or statistics based on predicted and observed responses. The proportion of concordant predictions (cases where predicted events agree with observed events) and discordant predictions illustrate the goodness of fit. There were 53 colonization events and 3086 nonevents. Colonization is positively related to the rate of decline of prey on nearest neighbor plants during the previous time interval, previous prey density on nearest neighbor plants (temporal lag 2), the rate of decline of prey on next-next-nearest neighbors, and on the previous prey density inhabiting plants not in the neighborhood of target plants (i.e., prey density on plants that are not in the region delineated by the next-next-nearest neighbors). The contribution from prey

TABLE 2. Analysis of super-island experiment: results from logistic regression analysis of colonization probability.

Colonization	Independent variables	Parameter estimates (P)	Percentage
Prey colonization, $\chi^2 = 150.9$ with 5 df ($P < 0.0001$)	Prey density on rest of plants	0.261 (0.0001)	
	Prey density on next nearest neighbors	0.0261 (0.020)	
	Prey density on nearest neighbors (lag 2)	0.0151 (0.002)	
	Rate of prey decline on nearest neighbors	0.047 (0.0006)	
	Rate of prey decline on next next-nearest neighbors	0.0699 (0.0007)	
	Intercept	−5.819 (0.0001)	
	Concordant predictions		83.1
	Discordant predictions		11.7
	Ties		5.2
Predator colonization, $\chi^2 = 49.7$ with 4 df ($P < 0.0001$)	Prey density on rest of plants (lag 1)	0.1006 (0.042)	
	Predator density on nearest neighbors	0.2022 (0.015)	
	Predator density on next nearest neighbors	0.6503 (0.0006)	
	Predator density on rest of plants (lag 2)	0.6051 (0.038)	
	Intercept	−2.9958 (0.0001)	
	Concordant predictions		79
	Discordant predictions		20.6
	Ties		0.4

Notes: Independent variables were averaged per plant and explicit neighbors defined. The best model was determined from both stepwise and backward elimination techniques.

not in the neighborhood is far greater than any of the other neighborhood contributions.

Predator colonization is positively related to local predator density (i.e., predator density on nearest and next-nearest neighbors), and the previous predator density on the rest of the plants (temporal lag 2). Colonization is not related to the local prey density, but is positively related to previous prey density on the rest of the plants (i.e., plants not in the neighborhood of the target). The regression coefficients describing predator contributions from various distances have the same order of magnitude. There were 46 colonization events recorded.

Analysis of metapopulation experiments

At the metapopulation level, colonization probability of prey and predators is highly variable over time (Figs. 4 and 5). The colonization probability of prey is relatively low at any given point in time (i.e., typically <0.1–0.15; maximum 0.35) in both experiments. Logistic spline fits to the dynamics of prey colonization shows cyclic variation with changing periodicity, and an upward trend during the last 100 d in system A and over the last 150 d in system B. Recall from Fig. 2 that while prey density fluctuates, it does not show systematic long-term changes in system A and declines in system B. Dynamics of predator colonization reflects the periodicity in prey colonization with a time lag of 2.5 wk in run A, and 2 wk in run B (estimated from a cross-correlation analysis of the splines). A major question is whether the temporal changes in colonization

probability can be accounted for solely by variation in state variables associated with densities of prey and predators at the various spatial scales.

Prey colonization of individual plants.—In metapopulation run A (Table 3), the colonization probability of prey was significantly ($P < 0.0001$) related to density of prey on nearest-neighbor plants, the rate of decline of prey on neighboring islands, and the previous density of prey (temporal lag 2) on the rest of the islands (i.e., non-neighboring islands). The nearest-neighbor variables positively influenced colonization (with the contribution from adjacent islands being higher than neighboring plants), while the lagged value of prey densities on more distant plants negatively affected the probability of colonization. It is interesting to note that colonization on target plants and prey density on the rest of the islands (temporal lag 2) also covary negatively based on simple correlation analysis ($P < 0.025$). Time also entered as a significant variable and had a positive effect on colonization probability.

There were 295 colonization events and 3794 non-events in system A. Nineteen of the colonization events occurred on islands with no prey present, 276 with prey already present on the island. Including prey presence as a covariate (0,1), leads to a similar model as presented in Table 3, except that prey presence simply replaces prey density on nearest neighbors as an explanatory variable and there is a slight improvement in goodness of fit (58% concordant prediction, 37.3% discordant predictions, 4% ties).

Prey colonization in system B (Table 3) was posi-

TABLE 3. Analysis of the two metapopulation experiments (system A and B): results from logistic regression analyses of colonization probability.

Colonization	Independent variables	Parameter estimates (P)	Percentage
System A			
Prey colonization, $\chi^2 = 28.3$ with 4 df ($P < 0.0001$).	Prey density on nearest neighbors	0.00621 (0.0009)	
	Rate of decline of prey on adjacent islands	0.0399 (0.0068)	
	Prey density on rest of islands (lag 2)	−0.0325 (0.028)	
	Date	0.0018 (0.0013)	
	Intercept	−2.816 (0.0001)	
	Concordant predictions		58.1
	Discordant predictions		38.8
	Ties		3.1
Predator colonization, $\chi^2 = 100.7$ with 6 df ($P < 0.0001$).	Local prey density	0.0075 (0.019)	
	Predator density on neighboring plants	0.154 (0.0001)	
	Predator density on island (lag 1)	0.199 (0.0003)	
	Rate of decline of predators on adjacent islands	0.027 (0.0097)	
	Prey density on island (distance 2, lag 2)	0.0022 (0.033)	
	Predator density on rest of system (lag 2)	0.496 (0.0008)	
	Intercept	−2.975 (0.0001)	
	Concordant predictions		68
	Discordant predictions		30.7
	Ties		1.3
System B			
Prey colonization, $\chi^2 = 41.6$ with 4 df ($P < 0.0001$).	Prey density on nearest neighbors (lag 1)	0.0094 (0.001)	
	Prey density on island	0.014 (0.004)	
	Prey density on next adjacent island (lag 2)	0.00174 (0.007)	
	Date	0.0011 (0.019)	
	Intercept	−3.1582 (0.0001)	
	Concordant predictions		57.2
	Discordant predictions		39.2
	Ties		3.6
Predator colonization, $\chi^2 = 136.5$ with 5 df ($P < 0.0001$).	Local prey density	0.0084 (0.008)	
	Predator density on neighboring plants (lag 2)	0.129 (0.0005)	
	Predator density on island (lag 1)	0.235 (0.0001)	
	Rate of decline of predators on rest of system	0.995 (0.0001)	
	Date	0.0012 (0.03)	
	Intercept	−2.963 (0.0001)	
	Concordant predictions		70
	Discordant predictions		28.4
	Ties		1.3

Note: Independent variables were averaged per plant and explicit neighbors defined.

tively related to time, the previous prey density on nearest neighbors (temporal lag 1), the density of prey on the island, and the previous prey density on the next-nearest islands (temporal lag 2). The coefficients for the local island effect were higher than the coefficient describing the next-adjacent island. In system B, there were 329 colonization events and 4365 nonevents. Twenty-six colonization events occurred on islands with no prey. Prey presence/absence did not significantly affect ($P > 0.05$) colonization probability.

Predator colonization.—The predator colonization probability in system A was positively related to local prey and predator densities, the previous predator density on the island (temporal lag 1), the rate of decline of predators on adjacent islands, and the previous density of predators on non-neighboring islands (temporal lag 2) (Table 3). The coefficient describing the contribution from predators on the rest of the system (i.e., more than two islands away) was higher than the local coefficient. Previous prey density on next-nearest neighbor islands (temporal lag 2) also had a significant positive effect on predator colonization. Of the 202
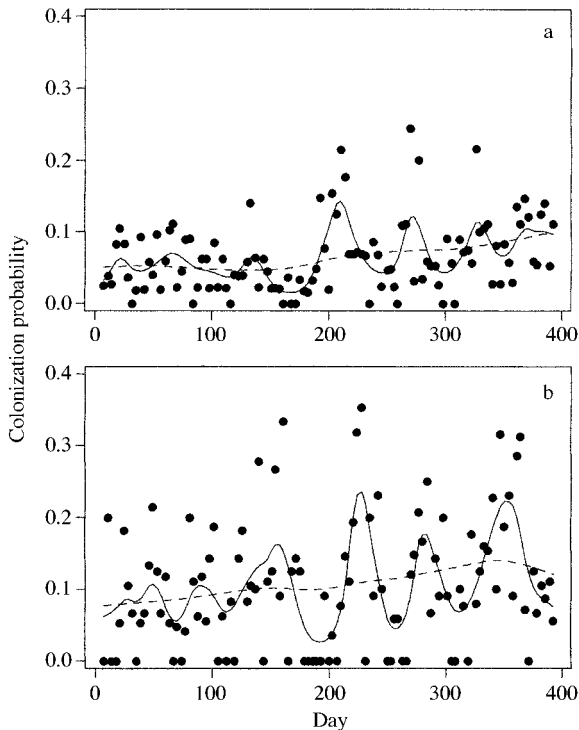
FIG. 4. Temporal changes in colonization probability of (a) prey and (b) predators in metapopulation system A. Lines are defined as in Fig. 3.

neighborhood suggests that prey dispersal is fairly large scale and not restricted to neighbors. In contrast, prey colonization in the metapopulation experiment (system A) is promoted when density on nearest neighbors is high or when prey are declining on adjacent islands. This suggests that the effect of subdividing the superisland and restricting dispersal via bridges is to create a spatial scale that is less than the system size. Despite the fact that young prey can easily cover several meters in a day in unrestricted systems (Helle and Sabelis 1985), we do not detect a contribution from the prey colonist pool on islands far from the target plant. This may allow for the development of asynchrony among islands. The negative lagged effect of prey density on the rest of the islands is difficult to interpret biologically, and it may simply reflect spatial asynchrony in the dynamics of islands widely separated in space. Given limited dispersal of prey, high prey density at one point in time on a particular island may reduce the colonization probability on islands far from the island with high prey density at that point in time. The results for the second metapopulation run are very similar to those from system A. The spatial scale for dependency of dispersal on prey density is primarily local (i.e., within island), or extends at most only two islands away.

The results also allow us to reject alternative models of the colonization process for prey and focus the rel-

colonization events, 69 occurred on islands with no predators present. The presence/absence of predators on the island was not a significant covariate.

The model structure for predator colonization in system B (Table 3) was similar to the model from system A, except that time was a significant factor. Predator colonization was positively related to local prey density, the previous predator density in the neighborhood (temporal lag 2), the predator density on the island (temporal lag 1), the rate of decline of predators on non-neighboring islands. There were 202 colonization events (2027 nonevents), and 86 of the colonization events occurred on islands without predators present. Including predator presence/absence as a covariate yields a model with the same number of variables and a slight reduction in the goodness of fit.

DISCUSSION

Our regression analysis detected local effects in the colonization of plants by prey and indicates how the spatial scale for dispersal of prey may have been modified by the spatial subdivision of the superisland into a metapopulation. In the super-island experiment, prey appear to be following the dispersal behavior identified from individual plant experiments (Janssen et al. 1997a). Prey leave the plants following peaks in adult prey density in the local neighborhood, and the larger relative contribution from prey on plants not in the
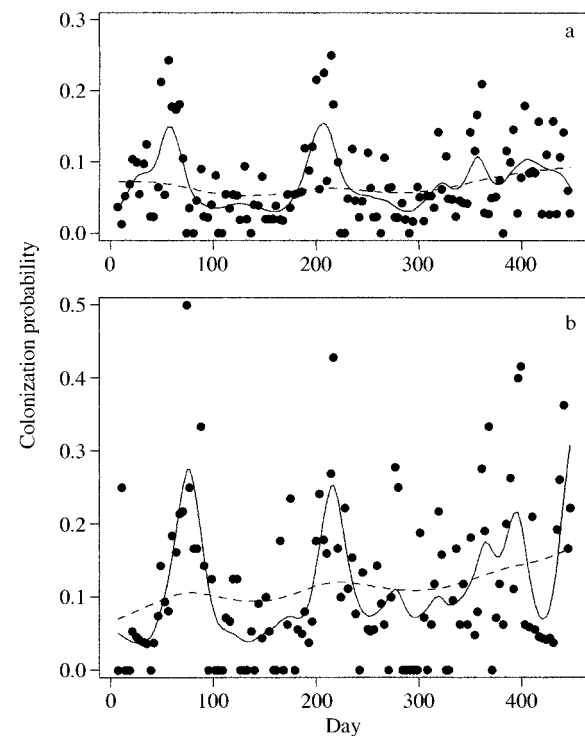

FIG. 5. Fluctuations over time in colonization probability of (a) prey and (b) predator in metapopulation system B. Lines are defined as in Fig. 3.

evant spatial scale to consider. For example, the local dependencies revealed by the regression analysis suggest that models of the colonization process merely based on a constant colonization probability for target plants or colonization rates based on only variation in global densities will likely be inadequate. It is clear that the probability of colonization of a plant is low, but if prey are present in the neighborhood or on adjacent islands then the probability is enhanced. This should not be interpreted as concluding that global dispersal of prey is not important; it could play a key role in potential dynamical mechanisms.

The spatial subdivision in the metapopulation experiment did not appear to introduce a restricted spatial scale less than the system size for predators: the models for predator colonization depend on both local densities and features of predator dynamics at the system level. Differences in the regression coefficients suggest that longer range effects are stronger than island level effects. There have been highly elaborate experiments performed on the chemical cues used by predators and prey (e.g., Sabelis and van de Baan 1983, Dicke et al. 1990, Janssen et al. 1997*b*, Dicke 1999, Janssen 1999) to both locate and avoid one another. It is not possible to detect some of the more subtle effects using the crude regression analysis (given the multicollinearity), but it is interesting to note that the logistic regression analysis of the metapopulation experiments detected a positive effect of predator colonization produced by high neighborhood densities of prey, independent of the local predator density. This effect is consistent with recent results from behavioral experiments (Zemek and Nachman 1998, Janssen 1999). Perhaps high neighborhood densities of prey increase the local concentration of prey volatile chemicals that are used by predators to locate aggregations of prey. Thus, a mechanistic model for predator colonization should include both local prey and predator densities, as well as an influence of global predator density.

One substantial change between the super-island and metapopulation experiments, was the overall decrease in the discovery rate of prey by predators. In this tritrophic system, prey densities can decline on plants either because they have been discovered (and consumed) by predators (predator–prey extinction events) or the prey can overexploit the plant and then emigrate from the site (plant–herbivore events). The proportion of plant–herbivore events can be compared to predator–prey extinctions to assess changes in discovery rate by predators in the different systems. In the super-island experiments, ~90% of prey populations on plants were driven extinct by the action of predators. In the metapopulation experiments, this dropped to 68% and 78% in systems A and B, respectively (i.e., the proportion of events that involve prey colonization, overexploitation of the host plant by prey, and dispersal of prey before being found by predators, increased in the

metapopulation experiment as a result of reducing the discovery rate of prey outbreaks by predators).

The contrast in results between the super-island and metapopulation experiments is quite revealing. Two aspects of colonization were affected by spatial subdivision and both of these effects have been shown to promote stability in predator–prey metapopulation: (1) reduction of the discovery rate of prey outbreaks on plants by predators systems (e.g., McLaughlin and Roughgarden 1992, McCauley et al. 1993), and (2) separation of dispersal scales for prey and predators (de Roos et al. 1998).

There were no striking qualitative differences in the comparison of regression models of colonization probability for prey or predators in the different runs of the metapopulation experiment (i.e., contrasting runs A and B). Local and among-island variables were similarly represented in prey models and in the respective predator models. This qualitative agreement (and the relatively small number of independent variables) is reassuring given the large number of candidate variables and their potential multicollinearity. The fact that we end up with virtually identical covariates for prey in the two separate runs, and predators in the two separate runs, reduces the likelihood that these covariates represent spurious correlations that might arise given the large number of candidate variables (i.e., the probability of getting the same spurious covariates included in two independent runs is low). If the data are combined from both runs for prey or for predators with a dummy variable to designate experimental run, covariates with the same biological interpretation are selected and the dummy variable is insignificant ($P > 0.05$). Thus, we have a relatively consistent empirical description and the likelihood that the variables chosen result from spurious correlations is low.

It is clear from the variable list and the time scale in the biology of predators and prey, that there is a considerable degree of multicollinearity among the independent variables. This does not artificially inflate our explanatory power, but it does limit our ability to arrive at the most biologically relevant model, since we have less information with which to evaluate the independent contribution of regressor variables. Fortunately, we did not encounter the most severe case of multicollinearity where the overall model is significant but none of the independent regressor variables are individually significant. Thus, while multicollinearity exists it most likely simply obscured our ability to evaluate alternative models and care needs to be taken in our quantitative interpretation of the independent contribution of variables. Our inferences regarding the relative contribution of local and global variables are based on considering only large differences between regression coefficients, and are robust against substantial changes in the critical P value used for variable selection (see Tables 2 and 3).

The observed lack of stationarity (time dependence)

in the colonization process for prey is not a result of changes in suitability of plants (recall that plant age did not enter significantly as an independent variable in any of the analyses of colonization probability), but it could be caused by systematic changes in the behavior of prey (i.e., when they disperse from plants) or their performance during dispersal (i.e., changes in survivorship crossing damp soil, locating bridges, etc). Prey colonization increased with time during both experimental runs (while global prey density either remained constant [system A] or decreased [system B]), and percent occupancy increased during the last half of each run. These systematic changes suggest that despite the fact that the fluctuations are relatively constant the system is not at equilibrium. These changes could arise from a variety of causes, such as simple behavioral changes, maternal effects, or natural selection producing changing parameters (e.g., Stokes et al. 1988). It is unclear both why these changes arose and whether these systematic changes had an effect on the dynamics of the metapopulation runs.

Answering the question as to how persistence was achieved in the metapopulation is beyond the scope of this paper since it requires alternative analytical models that embody the different mechanisms. However, the results from the regression models can be used to develop a mechanistic model of the colonization process, and once functional forms for the processes have been formulated the data could be used for parameter estimation (B. Kendall et al., *unpublished manuscript*). The model of colonization for the metapopulation has to capture the salient feature that prey dispersal is primarily local while predator dispersal is primarily large scale but possesses a significant within-island effect. The mechanistic description of colonization could then be used in alternative models of dynamics of predator–prey interactions in the metapopulation (S. Ellner et al., *unpublished manuscript*) to investigate how predominantly local prey dispersal interacts with more global predator dispersal to promote persistence or stability. Second, the regression models provide a series of probes (Kendall et al. 1999) that could be used to evaluate predictions from alternative metapopulation models that purport to account for the dynamics. For example, a metapopulation model whose dynamics are consistent with the observed major features (e.g., correct equilibria, persistence, etc.) could generate predicted data on the dynamics of prey and predators on individual plants in the metapopulation experiment with identical inoculation schedules plus some demographic stochasticity in success of these initial colonists. These artificial (fake) data could be analyzed by the same process we used on the experimental data (i.e., the logistic regression techniques), and these regressions should contain similar variables and dependencies as the empirical system. If they do not, then it suggests that the explanation offered by the model for the persistence may be different from the actual ex-

planation, since it has failed to capture the appropriate colonization phenomena.

Lessons learned from the analysis of detailed laboratory systems may help to guide the analysis of other laboratory and field studies. Experiments that measure dispersal are difficult, and perhaps the regression approach that we used here can be cautiously applied in field cases where crucial assumptions can be met, or at least their impact evaluated in separate experiments that are less difficult than those designed to measure actual dispersal rates. Wherever possible, direct observation of dispersal rates are preferred, but the regression approach we suggest may be useful in the development of models for colonization processes of both laboratory and field systems.

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