High Reproductive Rates Result in High Predation Risks: A Mechanism Promoting the Coexistence of Competing Prey in Spatially Structured Populations

Michio Kondoh[*]

Center for Ecological Research, Kyoto University, Otsuka, Hirano-cho, Kamitanakami, Otsu 520-2113, Japan

ABSTRACT: I tested the hypothesis that spatial structure provides a trade-off between reproduction and predation risk and thereby facilitates predator-mediated coexistence of competing prey species. I compared a cellular automata model to a mean-field model of two prey species and their common predator. In the mean-field model, the prey species with the higher reproductive rate (the superior competitor) always outcompeted the other species (the inferior competitor), both in the presence of and the absence of the predator. In the cellular automata model, both prey species, which differed only in their reproductive rates, coexisted for a long time in the presence of their common predator at intermediate levels of predation. At low predation rates, the superior competitor dominated, while high predation rates favored the inferior competitor. This discrepancy in the results of the different models was due to a trade-off that spontaneously emerged in spatially structured populations; that is, the more clustered distribution of the superior competitor made it more susceptible to predation. In addition, coexistence of competing prey species declined with increasing dispersal ranges of either prey or predator, which suggests that the trade-off that results from spatial structure becomes less important as either prey or predator disperse over a broader range.

Keywords: predator-mediated coexistence, spatial effect, apparent competition, exploitative competition, cellular automata, trade-off between predation risk and reproduction.

The promotion of species' coexistence remains a central question in ecology (e.g., Paine 1966; Levin and Paine

* Present address: Cardiff School of Biosciences, Cardiff University, P.O. Box 915, Cardiff CF10 3TL, United Kingdom; e-mail: kondoh@ecology.kyoto-u.ac.jp.

1974; Connell 1978; Tansky 1978; Tilman and Pacala 1993; Huston and DeAngelis 1994; Tilman 1994). In general, species that compete for the same resources do not coexist because the species that can survive at the lowest resource levels tends to eliminate the other species through exploitative competition (e.g., Tilman 1982). So how do species sometimes coexist on apparently similar resources in nature? Various hypotheses have been proposed to explain the coexistence of competing species, including the suggestion that predation or parasitism (hereafter referred to as "predation"; a parasitoid is also referred to as a "predator") enhances the coexistence of prey species (Paine 1966; Janzen 1970; Levin and Paine 1974; Caswell 1978; Connell 1978; Lubchenco 1978; Tansky 1978; Huston 1979; Teramoto et al. 1979; Hastings 1990; Pacala and Crawley 1992; Tilman 1994; Leibold 1996).

The predation hypothesis of species coexistence proposes at least three major mechanisms. First, predation can create a local refuge for inferior competitors by temporarily removing superior competitors (Caswell 1978; Hastings 1990; Pacala and Crawley 1992; Tilman 1994), thereby lowering the rate of competitive exclusion (Huston 1979). Second, a trade-off between competitive ability and resistance to predation (Lubchenco 1978; Gleeson and Wilson 1986; Pacala and Crawley 1992; Leibold 1996) can generate an advantage for the minority because the predator population increases as a result of the increasing abundance of the superior competitor (which is less resistant to predation pressure). Third, if a more abundant species is more susceptible to predation than a less abundant species (i.e., predator switching), the competing species can coexist without trade-offs because the behavior of the predator again provides an advantage to the minority (Tansky 1978; Teramoto et al. 1979; Gleeson and Wilson 1986; Pacala and Crawley 1992).

The objective of this study was to explore the effects of space and spatial structure (e.g., distribution, heterogeneity) on predator-mediated coexistence. The role of space in determining community architecture is undisputed

(e.g., Hanski and Gilpin 1997; Tilman and Kareiva 1997). Spatially finite dispersal and interactions alter and are influenced by the distribution patterns of interacting organisms. Such feedback between spatial distribution patterns and the intensity of biological interactions can potentially determine the structure of biological communities. For example, spatially finite dispersal and interactions result in a clumped distribution of sessile species (Pacala and Levin 1997) and increase the strength of intraspecific competition relative to interspecific competition, which leads to coexistence of the competing species (Shorrocks et al. 1979; Atkinson and Shorrocks 1981; Ives and May 1985; Pacala and Levin 1997). Such spatial effects can also modify prey-predator interactions. Spatially clustered prey may be more susceptible to predation if the intensity of predatory behavior increases with increasing local prey density (e.g., Hassell and May 1974; Connell 2000) or, similarly, when parasitoids are more easily transmitted between closely neighboring individuals (e.g., Sato et al. 1994).

Several theoretical models have considered predator-mediated coexistence in spatially structured habitats (Caswell 1978; Crowley 1979; Comins and Hassell 1996). Some studies (Caswell 1978; Crowley 1979) have investigated environments that consist of multiple patches, each of which is connected to all others, while other studies (Comins and Hassell 1996) have assumed a kind of diffusive dispersal within patchy environments by using a spatially explicit metapopulation model. These studies suggest that spatial structure allows for the persistence of interacting species, even if local dynamics do not allow their long-term coexistence, and that predator-mediated coexistence occurs in the presence of an explicit interspecific trade-off between some characteristics (e.g., reproduction and predation resistance, dispersal rate and growth rate, dispersal rate and predation resistance). However, it is still unclear how high mortality due to clustering affects predator-mediated coexistence because previous studies either did not assume an explicit space (Caswell 1978; Crowley 1979) or focused on processes at larger spatial scales (e.g., metapopulations; Comins and Hassell 1996).

In this article I report a new finding: spatial structure provides a trade-off between reproduction and predation risk and therefore effectively promotes predator-mediated coexistence of two competing species that differ only in their reproductive rates. I have assumed that the spatial structure is sufficient for the two competing prey species to coexist in the presence of a common predator.

I compared a mean-field model and a cellular automata model of two prey species and their common predator in a patchy environment. A mean-field model assumes spatially well-mixed individuals, while a cellular automata model is based on the individual and assumes spatially limited dispersal of individuals. In the mean-field model,

coexistence does not occur if we do not assume an explicit trade-off between reproductive (or mortality) rate and predation resistance. In contrast, in the cellular automata model, coexistence is possible even if neither an explicit trade-off nor predator switching occurs, both of which have been considered essential to predator-mediated coexistence. This is because the superior competitor with the higher reproductive rate has a more clustered distribution and is therefore more susceptible to predation by a predator whose offspring disperse locally.

I considered a habitat composed of distinct resource patches for which two prey species (prey 1 and 2) compete. Each patch is occupied by prey 1 (superior competitor) or prey 2 (inferior competitor) or the predator, unless it is unoccupied. Assume that prey and predator species are sessile and that movement of individuals only occurs once at the offspring stage. The dynamics of patch occupancy for each species are determined by the stochastic processes of interpatch colonization via dispersal and extinction within a patch. Local extinction for predator and prey species occurs at fixed rates (mortality rates; prey $i \rightarrow$ empty, predator $\rightarrow$ empty). The offspring of prey species disperse to other patches (i.e., colonization) at a constant rate (colonization or reproductive rate of prey) and only succeed if they disperse to empty patches (prey $i +$ empty $\rightarrow 2[\text{prey } i]$). A reproductive rate of prey is a product of a number of offspring produced from a prey patch and the possibility of successful establishment when the prey arrives at an empty patch. Predator colonization occurs at a fixed rate (colonization or predation rate of predator) and can only be successful if the new patch is already occupied by a prey species; following colonization by a predator, the prey is subject to predation to extinction and the predator becomes established in that patch (predator + prey $i \rightarrow 2[\text{predator}]$). Predation rates can have prey-specific values depending on whether or not the predator, which arrives at a focal prey's patch, successfully establishes in that patch. To avoid a coexistence realized as a result of explicit trade-offs between fitness components such as reproduction, mortality due to natural death, or predation resistance, the models are presented using parameter sets describing conditions wherein the two prey species have different reproductive rates but the same mortality and predation rates.

The Mean-Field Model

I considered a habitat composed of a large number of distinct patches. I assumed that a species is able to colonize any patch, whatever its distance; in other words, every resource patch is accessible to every individual, whether prey or predator. Assuming an infinite number of patches,

the frequency of patch occupation by each respective species is calculated as follows:

$$\frac{dx_1}{dt} = r_1 x_1 (1 - x_1 - x_2 - y) - mx_1 - cx_1 y, \quad \text{(1a)}$$

$$\frac{dx_2}{dt} = r_2 x_2 (1 - x_1 - x_2 - y) - mx_2 - cx_2 y, \quad \text{(1b)}$$

$$\frac{dy}{dt} = c(x_1 + x_2)y - dy, \quad \text{(1c)}$$

where x_i (where $i = 1$ or 2) and y are the frequencies of patch occupation by prey i and the predator, respectively; r_i is the colonization or reproductive rate of prey i ($r_1 > r_2$; prey 1 is the superior competitor, prey 2 the inferior competitor); c is the colonization rate by the predator of patches occupied by prey (predation rate); and m and d are the mortality rates of prey and predator, respectively.

The possible equilibrium and species frequency at each equilibrium are obtained as follows: $(x_1^*, x_2^*, y^*) = $ (i) $(d/c, 0, \{r_1[1 - (d/c)] - m\}/[c + r_1])$ for prey 1 and predator coexistence; (ii) $(0, d/c, \{r_2[1 - (d/c)] - m\}/[c + r_2])$ for prey 2 and predator coexistence; (iii) $(1 - [m/r_1], 0, 0)$ for prey 1 alone; (iv) $(0, 1 - [m/r_2], 0)$ for prey 2 alone; (v) $(0, 0, 0)$ for no species persistence. Equilibrium ii is unstable because such a community is always invaded by prey 1. Equilibrium iv is also locally unstable because such a community is again invaded by prey 1. Equilibrium i is stable if and only if $[1 - (d/c)] > (m/r_1)$; equilibrium iii is stable if and only if $1 > (m/r_1) > [1 - (d/c)]$; equilibrium v is stable if and only if the ratio of the mortality rate to the reproductive rate of both prey species is sufficiently high ($[m/r_1] > 1$; see appendix for a more detailed analysis).

There is no equilibrium in which the two prey species coexist, which suggests that two prey species with different reproductive rates ($r_1 > r_2$) and the same mortality rate (m) cannot coexist with any stability if their predation rates are the same (c), as pointed out by previous models of one-predator-two-prey systems without explicit space (Cramer and May 1972; Fujii 1977; Tansky 1978; Teramoto et al. 1979).

The Cellular Automata Model

Predator-Mediated Coexistence in Spatially Structured Habitats

In order to investigate a situation in which colonization occurs as a local process, I used a cellular automata model of one predator and two prey species. Population dynamics were examined by using an individual-based model. The habitat was a torus composed of $N \times N$ sorted patches. Each simulation was initiated with a random distribution and frequency of two prey and one predator species. Unit time step (T) consisted of $N \times N$ sets of the following steps:

Step 1. Choose a patch (patch 1) at random. If the patch is occupied, specify a neighboring patch (patch 2) and proceed to step 2. The neighboring patches are in some cases the four adjacent cells; in other cases they are a larger number of nearest cells. If patch 1 is empty, skip step 2 and proceed to step 3.

Step 2. If patch 2 cannot be colonized, proceed to step 3. If patch 1 is occupied by either prey species and patch 2 is empty, then prey i in patch 1 may colonize the empty patch 2. The empty patch becomes occupied by prey i with probability r_i (≤ 1). If patches 1 and 2 are predator and prey patches, respectively, the predator may colonize the prey patch; the prey patch becomes a predator patch with probability c (≤ 1).

Step 3. Choose a patch at random. If an organism occupies this patch, it will become extinct with a fixed probability; a prey and a predator patch become empty with probabilities m (≤ 1) and d (≤ 1), respectively. The mortality probability of the predator and prey used for all examples presented is $(d, m) = (0.04, 0.028)$.

Suppose that frequencies of prey 1, prey 2, and the predator are given by x_1, x_2, and y, respectively. If the neighboring patches are the entire space, the rate of prey i's colonization is given by the following formula: the probability that prey i is chosen in step 1 × the probability that the empty patch is chosen in step 2 × the probability that prey i colonizes the empty patch; that is, $r_i x_i (1 - x_1 - x_2 - y)$. Similarly, the rate of the predator's colonization is given by $cy(x_1 + x_2)$. The mortality rate of a species is given by the following formula: the probability that the species is chosen in step 3 × the probability that the species become extinct; that is, mx_i and dy for prey i and the predator, respectively. These rates are identical to those in the mean-field model, which suggests that the probabilities r_i, c, m, and d are analogous to the rates r_i, c, m, and d in the mean-field model in a small-time step of a set of steps 1–3. For predation rates >1 ($c > 1$), I used an approximation by having the probability $c/2$ and doubling steps 1 and 2 for the predation process only. If the neighboring patches are the entire space, this approximation gives the predation rate by

$$\{(c/2)y(t)[1 - x_1(t) - x_2(t) - y(t)]\}$$

$$+ \{(c/2)y(t + \Delta t)[1 - x_1(t + \Delta t) - x_2(t + \Delta t) - y(t + \Delta t)]\},$$

which suggests that this procedure gives a good approximation if the change in patch frequencies within a time step (Δt) is small.

First, the simplest case, where colonization is always

4 neighbors for prey and predator
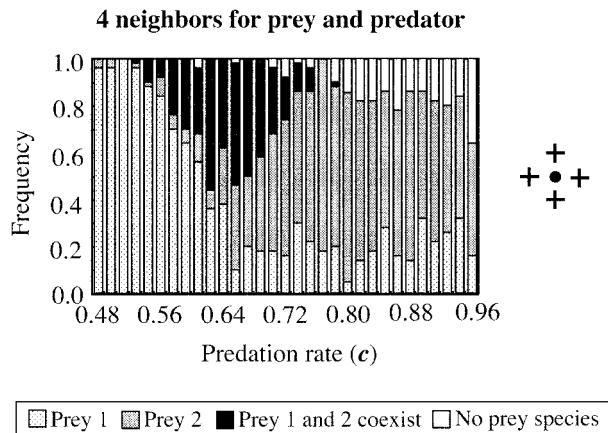
Figure 1: Competitive outcomes plotted against predation rates when all species colonize four neighboring patches. The frequency of species composition (prey 1, prey 2, or their coexistence) at $T = 10,000$ is represented. Each bar represents a predation rate ($c = 0.48$ to 0.96 in increments of 0.016). Resulting outcomes are that two prey species coexist (*black*), prey 1 outcompetes prey 2 (*light gray*), prey 2 outcompetes prey 1 (*dark gray*), or no prey species persists (*white*). I ran 50 simulations for each predation rate. The space is composed of 150 × 150 patches. Other parameters are $(r_1, r_2, m, d) = (0.16, 0.112, 0.028, 0.04)$.

restricted to the four nearest neighborhoods, was considered. In the absence of predation, if the two prey species have different reproductive rates ($r_1 = 0.16$; $r_2 \leq 0.136$), then prey 1 (the superior competitor) outcompetes prey 2 (the inferior competitor) within 10,000 time steps in all 50 simulations. When the two species are assigned similar reproductive rates ($r_1 = 0.16$; $r_2 > 0.136$), the inferior competitor may not be eliminated within the simulation time (this occurred in two out of 50 simulations for $r_2 = 0.144$ and 17 out of 50 simulations for $r_2 = 0.152$). However, even in these cases, the inferior competitor eventually becomes extinct after a longer simulation run.

In the presence of a predator, a completely different picture emerges (fig. 1). Depending on the predation rate (c), one prey species outcompetes the other in some cases, while in other cases long-term coexistence of the two competing prey species is observed. The predator-mediated coexistence of both prey species occurs only when c is intermediate ($c = 0.496$ to 0.768 in fig. 1). At low predation rates, the inferior competitor is hardly able to persist, whereas at high predation rates, the superior competitor tends to become extinct. Although the frequency of predator extinction due to demographic stochasticity increases with increasing predation rates, the predator population always persists when two prey species coexist. Figure 2 shows examples of the population dynamics for the respective outcomes. Coexistence was observed in a wide range of r_1/r_2, although it did not occur when r_1 was

much larger than r_2. For a parameter set of $(r_1, c, m, d) = (0.16, 0.64, 0.028, 0.04)$, for example, coexistence was observed in 19–28 out of 50 simulations for $r_2 = 0.08$ to 0.144, while it was not observed at all for $r_2 < 0.064$. The pattern in which a high predation rate favors the inferior competitor was robust to variations in initial conditions and parameters.

Spatial Distribution Patterns and Susceptibility to Predation

The result that high predation rates favor the inferior competitor suggests that the superior competitor is more likely to be attacked by a predator (i.e., more susceptible to predation) than the inferior competitor. To confirm the hypothesis that coexistence is due to a higher susceptibility
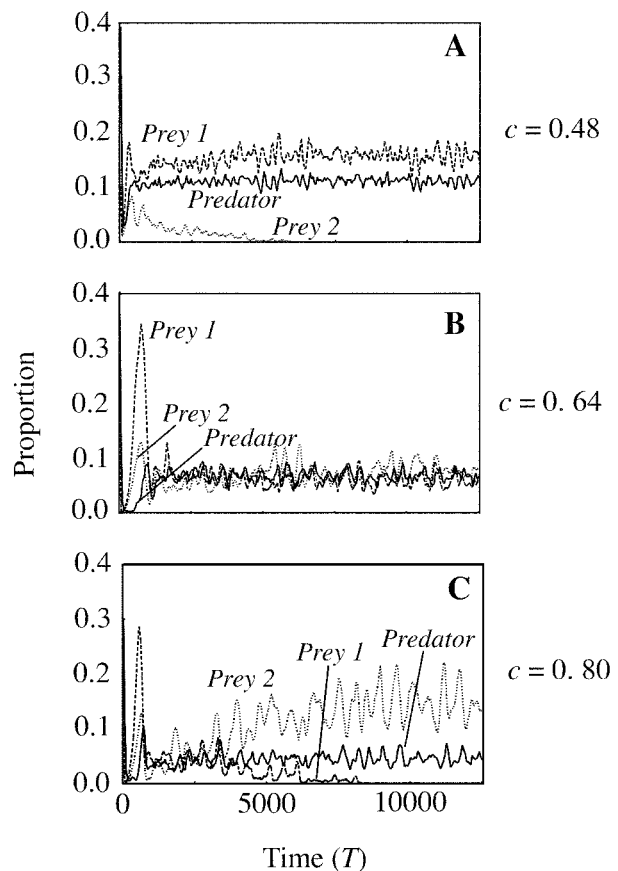

Figure 2: Examples of the population dynamics of two prey species and a predator when each species colonizes four neighboring patches. Dashed, dotted, and solid lines represent populations of prey 1 (the superior competitor), prey 2 (the inferior competitor), and their common predator, respectively. Predation rate, *c*, for each simulation is (*A*) 0.48, (*B*) 0.64, and (*C*) 0.8. Grid size and other parameters are described in figure 1.

of the superior competitor to predation resulting from its more clumped distribution pattern, I examined the spatial distribution patterns of the two prey species and the susceptibility of these prey species to predation.

One measure of clustering is a comparison of the local density (which is identical to "mean crowding" by Lloyd 1967), defined as the mean density of neighbors experienced by an individual (P_1, P_2) and the mean density (x_1, x_2) over the whole space (global density). The ratio of local density to global density is expected to increase with increased clustering and should be 1.0 for randomly distributed individuals (e.g., Lewis 1997). During simulation, the local density (P_i) was always higher than the global density (x_i) for both prey 1 and prey 2 (fig. 3A), which suggests that both prey species showed a clustered distribution pattern (fig. 3B). Moreover, for the same global density, the local density of the superior competitor was higher than that of the inferior competitor (fig. 3A), which implies that the superior competitor had a more clumped distribution than the inferior competitor.

The susceptibility (S_i) of prey i to predation is defined as the number of predation events on prey i per unit of time ($N \times N$ sets of steps 1–3) divided by the average number of prey i during the one-unit time step. If the two species are equally preyed upon, S_i should be the same for both prey 1 and prey 2 and should be proportional to (cy). The bias of predation pressure between prey 1 and prey 2 can be obtained by comparing their respective susceptibilities, S_1 and S_2. Simulations showed a general tendency for the susceptibility of the superior competitor to be higher than that of the inferior competitor (fig. 4). This implies that, as expected, the superior competitor is more susceptible to predation than the inferior competitor.

These results explain why prey species with different reproductive rates can coexist in the presence of a predator in a spatially structured habitat. Since colonization by each prey species is a local process, both species show a clustered distribution in space (fig. 3). In such a clustered distribution, once the predator has invaded a cluster of prey, it is then more likely to colonize local patches of the same prey. The superior competitor, which has a higher growth rate (or a lower mortality), tends to be more clumped (as suggested by its high local density, P_i) than the inferior competitor; that is, there are more empty sites that cannot be traversed by the predator in clusters of the inferior competitor than in those of the superior competitor (fig. 3). Thus, because of the slow advance of the predator population in the inferior competitor's clusters, it follows that the superior competitor is more susceptible to the predator than the inferior competitor (fig. 4). A trade-off between reproduction and predation risk emerges.
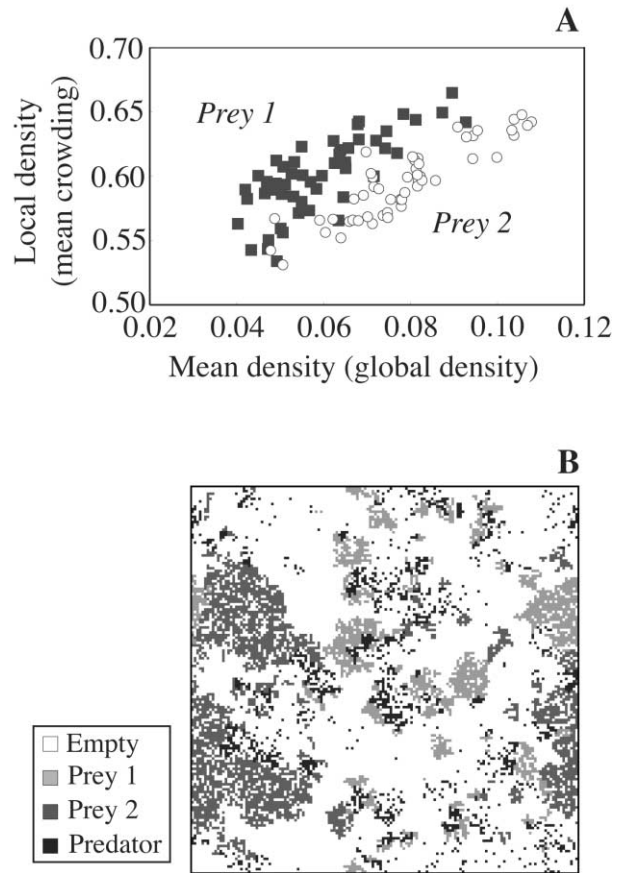
Figure 3: *A*, Local densities of prey 1, P_1 (*filled squares*), and prey 2, P_2 (*open circles*), plotted against mean densities of respective prey for a simulation run (T = 10,000 to 12,500 in increments of 50) in which two prey species coexist (c is set to 0.64). Prey and predator each colonize four neighboring patches. *B*, Snapshot of a simulation of the cellular automata model when each species colonizes four neighboring patches (T = 9,500, c = 0.64). Each point represents an empty patch (*white*), a prey 1 patch (*light gray*), a prey 2 patch (*dark gray*), or a predator patch (*black*). Space size, initial conditions, and other parameters used in these two panels are described in figure 1.

Dispersal Distance and Predator-Mediated Coexistence

The situation when dispersal is not limited to the four nearest neighboring patches is now investigated. If the predation that is biased toward the superior competitor is caused by the superior competitor's clumped distribution patterns, then wider dispersal by prey species is predicted to inhibit predator-mediated coexistence for two reasons. First, dispersal lowers the local density of prey, which reduces the predation rate and makes it difficult for the predator to persist. Second, the benefit of having a low reproductive rate (i.e., a low predation risk) is reduced because with wider dispersal ranges, prey species show a
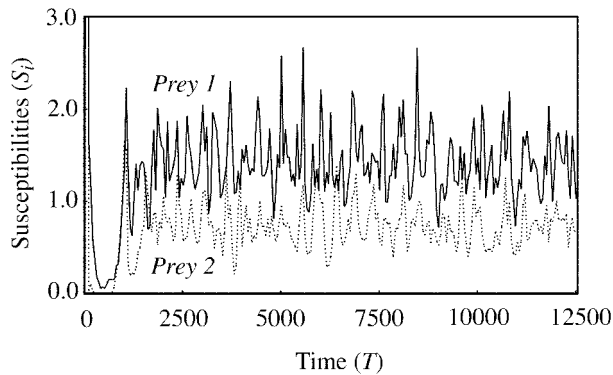
Figure 4: Susceptibilities of prey 1, S_1 (*solid line*), and prey 2, S_2 (*dotted line*), for a simulation run in which two prey species coexist ($c = 0.64$). Both prey and predator colonize four neighboring patches. Space size, initial conditions, and other parameters used are described in figure 1.

less clustered distribution even if their reproductive rates are high.

Consider the case in which both prey species colonize more patches (eight or 24 neighbors) while the offspring of the predator disperse only to the four nearest sites. Simulations suggested that predator-mediated coexistence becomes difficult as the number of available sites neighboring a prey site increases (cf. the frequency of "Prey 1 and 2 coexist" in fig. 5*A* with that in fig. 1) and is not observed for colonization of 24 neighboring patches (fig. 5*B*). With prey colonization of an increased number of neighboring sites, the predation rate needed to maximize the probability of coexistence increases; it is near $c = 0.624$ in the case of four neighbors (fig. 1) and near 1.008 for eight neighbors (fig. 5*A*) because the dispersal of prey lowers its local density and decreases the effective colonization rate of the predator.

Wider dispersal by the predator also invalidates the trade-off between reproduction and predation risk. Consider the case in which the predator disperses more widely while the prey colonizes only the four nearest patches. Simulations suggested that coexistence becomes difficult with an increase in the number of sites neighboring a predator site (cf. the frequency of "Prey 1 and 2 coexist" in fig. 6 with that in fig. 1). This is because a low local prey density does not reduce the prey's susceptibility to predation, since the predator can skip empty patches, and its propagation then tends not to be inhibited by low local density of prey species. Furthermore, the predation rate that maximizes the probability of coexistence decreases with an increase in the number of neighboring sites occupied by predators ($c = 0.528$ and 0.48 for eight and 24 neighbors, respectively). This can be explained as follows: if the predator population persists in clusters, a predator

that disperses locally tends to encounter patches already occupied by another predator and therefore experiences low prey availability. Thus, wide dispersal increases the effective dispersal rate of the predator and lowers the predation rate that results in the maximum probability of coexistence.

Dispersal distance is clearly an important factor influencing the effect of a predator on competitive outcomes. The trade-off between reproduction and predation risk that results from spatial structure becomes less important when either prey or predator disperses over a broader range. A prey species that colonizes more widely and has a less clustered distribution is less susceptible to predation even if it has a high reproductive rate, while a predator
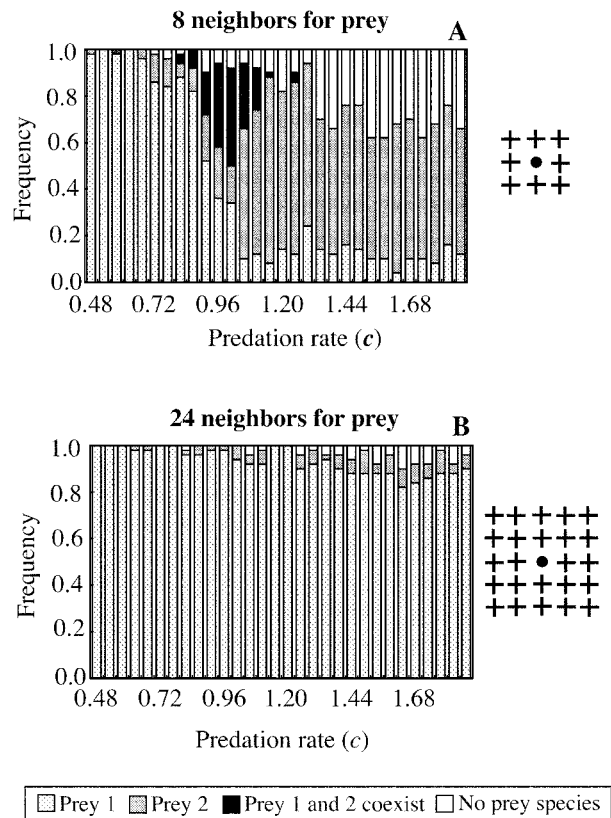
Figure 5: Competitive outcomes when both prey have wide dispersal ranges. Panels show the results when prey are assumed to colonize eight (*A*) and 24 (*B*) nearest neighboring patches. The frequency of species composition (prey 1, prey 2, their coexistence, or extinction of both prey species) at $T = 10,000$ is represented. Each bar represents a predation rate ($c = 0.48$ to 1.872 in increments of 0.048). Resulting outcomes are such that two prey species coexist (*black*), prey 1 outcompetes prey 2 (*light gray*), prey 2 outcompetes prey 1 (*dark gray*), or no prey species persists (*white*). I ran 50 simulations for each parameter set. Space size and initial conditions are described in figure 1. Parameters are $(r_1, r_2, m, d) = (0.16, 0.112, 0.028, 0.04)$.
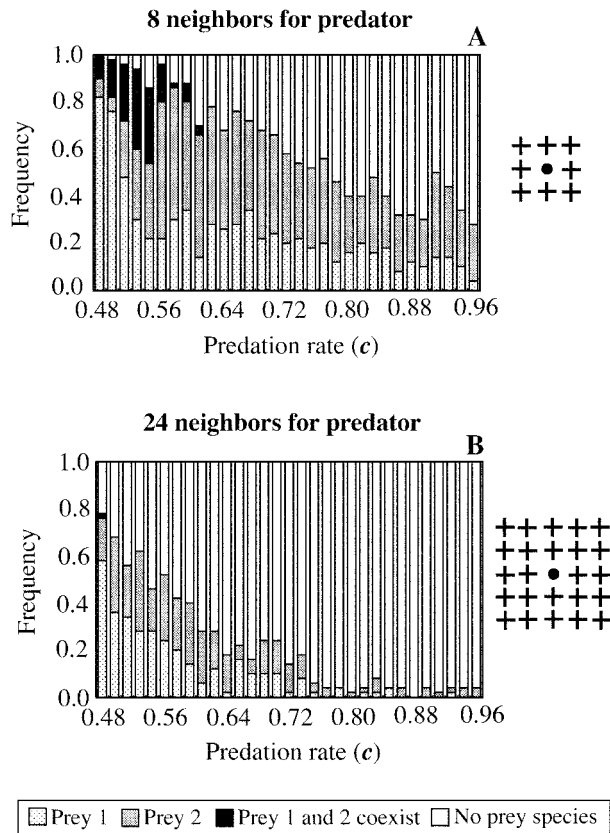
Figure 6: Competitive outcomes when predator has wide dispersal range. Panels *A* and *B* show the results when the predator colonizes eight and 24 neighboring patches, respectively. The frequency of species composition (prey 1 alone, prey 2 alone, their coexistence, or extinction of both prey species) at $T = 10,000$ is shown. Each bar represents a predation rate ($c = 0.48$ to 0.96 in increments of 0.016). Resulting outcomes are that two prey species coexist (*black*), prey 1 outcompetes prey 2 (*light gray*), prey 2 outcompetes prey 1 (*dark gray*), or no prey species persists (*white*). I ran 50 simulations for each predation rate. Space size, initial conditions, and other parameters are described in figure 1.

with greater mobility can traverse unoccupied sites and therefore be less affected by prey distribution. Such a predator reduces the possibility of coexistence. In an extreme case in which all species have an infinitely wide dispersal range (which corresponds to the mean-field model), predator-mediated coexistence does not occur at all.

Discussion

The simulations showed that despite the same predation rate being assigned, competing species can coexist in the presence of a common predator in spatially structured habitats. Two prey species cannot coexist either in a spatially less constructed model (i.e., a mean-field model or a cellular automata model with wide dispersal ranges) in

the presence of a common predator or in a cellular automata model in the absence of a predator. This suggests that spatial structure and a common predator are both essential to the coexistence observed in this model. This is very different from the assertion that intraspecific aggregation, which increases the intensity of intraspecific competition relative to that of interspecific competition, is sufficient for the coexistence of species with different competitive abilities (Shorrocks et al. 1979; Atkinson and Shorrocks 1981; Ives and May 1985; Pacala and Levin 1997). Instead, coexistence is due to local dispersal and interactions that provide a trade-off between reproduction and predation risk (i.e., the higher susceptibility of the superior competitor to predation) through the formation of spatial distribution patterns. Such a trade-off explains why a higher predation rate favors the inferior competitor, which has a low predation risk and a low growth rate, while the superior competitor, which has a high growth rate and a high predation risk, outcompetes the inferior competitor when predation rates are reduced (fig. 1).

The trade-off emerging in a spatially structured model suggests that an increase in reproductive rates of prey species can have the opposite effect on the prey's abundance depending on the spatiotemporal scale to be considered (e.g., Levin and Pimentel 1981). In cellular automata models, localized dispersal and interaction lead to segregated distribution of prey species. This implies that the whole system can be viewed as being divided into prey-predator subsystems, each of which includes either prey 1 or prey 2. In a spatial scale smaller than this prey's cluster (e.g., consider three sequential patches: prey 1–empty–prey 2), the prey with a high growth rate is more advantageous than that with a low growth rate because they occupy empty patches more quickly. In a large scale, however, the prey with a higher reproductive rate is more susceptible to predation because of its higher local density. In a small spatial scale, prey with high growth rates is more advantageous, while selection may favor prey with low growth rates in a large spatial scale.

The trade-off between reproduction and predation risk is a consequence of the distribution patterns of prey and the local dispersal of the predator. Richards et al. (1999) presented prey-predator models and found that an intermediate reproductive (or mortality) rate of a prey species evolves in a spatially explicit (one dimensional) model, while natural selection favors a higher reproductive rate (or a lower mortality rate) in a spatially implicit (well-mixed) model. Although the authors did not focus on mechanisms of coexistence, their results can be related to the trade-off between reproductive rate and predation risk that emerges in cellular automata models. A high reproductive (or low mortality) rate increases the predation risk, while a low reproductive (or high mortality) rate lowers

the competitive ability of the prey to occupy space. Natural selection therefore favors an intermediate reproductive (or mortality) rate for prey. It is clear that the mechanisms operating in the model of Richards et al. (1999) are the same as those presented in this article, although their model is limited to an extreme case in which disease propagates at a rate that is much faster than colonization by prey (i.e., the colonization rate of the predator is infinitely high: $c = \infty$). My model shows that an inferior competitor is favored by a high predator colonization rate, which suggests that the fast predator propagation in the model of Richards et al. (1999) maximizes the benefit of low susceptibility to predation that results from a low reproductive rate.

It has been hypothesized that an individual within an aggregation has a relatively low risk of predation (a low per capita predation rate; Vulinec 1990; Connell 2000). For example, schooling of fish has been considered a strategy to reduce the chance of being attacked by predators (references in Connell 2000). This is in striking contrast to my result, which suggests that a more aggregated prey species has a higher susceptibility to predation. The relative spatiotemporal scale by which the predator reproduces or disperses could explain the discrepancy between the two hypotheses. In general, the per capita predation rate is determined by the number of prey taken per predator and the number of attacking predators. Predators with a low mobility (e.g., passively transmitted parasites with low infection rates) tend to have a higher predation (infection) rate within aggregated prey (host) individuals (i.e., the number of prey taken per predator is positively density dependent). Further, predators with a short life cycle multiply quickly within an aggregation; that is, the number of attacking predators may also be positively density dependent. In such cases aggregation would increase the per capita attack rate. In contrast, even within more clustered prey, the numbers of predators with a longer life cycle or a higher mobility (e.g., mammals preying on fish) do not increase within the prey cluster (i.e., the number of attacking predators is not density dependent), and the number of prey taken per predator may become saturated (i.e., the number of prey taken per predator is less positively density dependent). Thus, it is predicted that aggregation lowers the risk of predation in such cases (but see Connell [2000] and Hassell and May [1974], who describe how aggregation increases the per capita predation rate if the predator responds more to a larger aggregation of prey; in such cases high mobility may not reduce the per capita predation rate).

A trade-off between reproduction and predation risk in general allows two competing species to coexist because it confers an advantage to the minority (Cramer and May 1972; Fujii 1977; Tansky 1978; Teramoto et al. 1979). An-

other possible mechanism by which predation promotes coexistence, which is not, however, mutually exclusive with the former mechanism, is that predation lowers the intensity of competition by increasing mortality, therefore slowing the rate of competitive exclusion and prolonging the time required for competitive exclusion to occur (nonequilibrium coexistence; Caswell 1978; Huston 1979). Caswell (1978) studied a well-mixed version of a patch model of two prey species and their common predator and demonstrated the possibility of such long-term predator-mediated coexistence. However, this mechanism is not independent of the characteristics of the competing species (Crowley 1979). It is obvious that a trade-off between reproduction and predation risk resulting from spatial structure would make nonequilibrium coexistence more possible; by increasing the mortality rate of the species with the higher reproductive rate, predation yields similar net growth rates for two species that have different reproduction rates.

Spatial structure may play an important role in shaping community structure. Theoretical studies (Nee and May 1992; Tilman et al. 1994; Comins and Hassell 1996; Pacala and Levin 1997) have shown how spatial structure affects either interspecific exploitative competition over resources or interspecific apparent competition (Holt 1977). Although some assumptions are simplified, by incorporating these two types of competition within a single model, the model presented here shows how they interact with each other in a spatially structured environment. The superior competitor in exploitative competition (i.e., the species with a high reproductive rate) tends to be the inferior competitor in apparent competition (the species with a high predation risk) for spatial distribution patterns, and spatial structure may therefore enhance the coexistence of competing prey species without assuming any explicit trade-offs.

Acknowledgments

APPENDIX

Stability Analysis of Population Dynamics

By setting the right-hand side of equations (1) to zero, the possible equilibrium and species frequency at each equilibrium are obtained as follows: $(x_1^*, x_2^*, y^*) = $ (i)

$(d/c, 0, \{r_1[1 - (d/c)] - m\}/[c + r_1])$ for prey 1 and predator coexistence; (ii) $(0, d/c, \{r_2[1 - (d/c)] - m\}/[c + r_2])$ for prey 2 and predator coexistence; (iii) $(1 - [m/r_1], 0, 0)$ for prey 1 alone; (iv) $(0, 1 - [m/r_2], 0)$ for prey 2 alone; (v) $(0, 0, 0)$ for no species persistence. Among them either equilibrium i, iii, or v can be locally stable, depending on parameters. A proof by local stability analysis follows.

Equilibrium i is feasible if and only if it holds that $1 - (d/c) - (m/r_1) > 0$. This equilibrium is locally stable if the real parts of all the eigenvalues of the following Jacobian matrix **S** around the equilibrium are negative (see May 1973):

$$
\mathbf{S} = \begin{bmatrix} \dfrac{d\dot{x}_1}{dx_1} & \dfrac{d\dot{x}_1}{dx_2} & \dfrac{d\dot{x}_1}{dy} \\[2ex] \dfrac{d\dot{x}_2}{dx_1} & \dfrac{d\dot{x}_2}{dx_2} & \dfrac{d\dot{x}_2}{dy} \\[2ex] \dfrac{d\dot{y}}{dx_1} & \dfrac{d\dot{y}}{dx_2} & \dfrac{d\dot{y}}{dy} \end{bmatrix}^*
$$

$$
= \begin{bmatrix} -r_1 x_1^* & -r_1 x_1^* & -(r_1 + c)x_1^* \\[1ex] 0 & \left(\dfrac{1}{r_1} - \dfrac{1}{r_2}\right)(m + cy^*) & 0 \\[1ex] cy^* & cy^* & 0 \end{bmatrix}.
$$

$$(A1)$$

Eigenvalues (λ) are given as solutions of $|(\mathbf{S} - \lambda E)| = 0$, that is, rewritten as

$$
\left[\left(\dfrac{1}{r_1} - \dfrac{1}{r_2}\right)(m + cy^*) - \lambda\right]\left[\lambda^2 + (r_1 x_1^*)\lambda + c(r_1 + c)x_1^* y^*\right] = 0.
$$

$$(A2)$$

Since $[(1/r_1 - 1/r_2)(m + cy^*)] < 0$, $r_1 x_1^* > 0$, and $c(r_1 + c)x_1^* y^* > 0$, it follows that all real parts of solutions λ should be negative. This equilibrium should be locally stable.

Equilibrium ii requires that $[1 - (d/c) - (m/r_2)] > 0$ to be feasible. It is, however, always unstable because such a community is always invaded by prey 1, as confirmed by the fact that a small fraction of prey 1 always increases within an equilibrium community of prey 2 and the predator, that is,

$$
\left.\dfrac{(dx_1/dt)}{x_1}\right|_{x_1=0,\, x_2=x_2^*,\, y=y^*} = \left(\dfrac{r_1}{r_2} - 1\right)(m + cy^*) > 0.
$$

Equilibrium iii is feasible if and only if it holds that $1 > (m/r_1) > [1 - (d/c)]$. By the same steps taken for equilibrium i, Jacobian matrix **S** around the equilibrium is given by

$$
\mathbf{S} = \begin{bmatrix} -r_1 x_1^* & -r_1 x_1^* & -(r_1 + c)x_1^* \\ 0 & r_2 - m - r_2 x_1^* & 0 \\ 0 & 0 & -d + cx_1^* \end{bmatrix}. \quad (A3)
$$

Then, eigenvalues (λ) are given as solutions of the following equation:

$$
(r_1 x_1^* + \lambda)\left[m\left(\dfrac{r_2}{r_1} - 1\right) - \lambda\right]\left[c\left(1 - \dfrac{m}{r_1} - \dfrac{d}{c}\right) - \lambda\right] = 0.
$$

$$(A4)$$

Since $r_1 x_1^* > 0$, $m(r_2/r_1 - 1) < 0$, and $c(1 - m/r_1 - d/c) < 0$, it follows that all real parts of solutions λ should be negative. This system is locally stable around the equilibrium.

Equilibrium iv requires a condition in which $(1 - m/r_2) > 0$ to be feasible. This equilibrium is, however, locally unstable because such a community is always invaded by prey 1, as confirmed by

$$
\left.\dfrac{(dx_1/dt)}{x_1}\right|_{x_1=0,\, x_2=x_2^*,\, y=0} = \left(\dfrac{r_1}{r_2} - 1\right)m > 0.
$$

Equilibrium v is always feasible. In this case, Jacobian matrix **S** is given by

$$
\mathbf{S} = \begin{bmatrix} r_1 - m & 0 & 0 \\ 0 & r_2 - m & 0 \\ 0 & 0 & -d \end{bmatrix}. \quad (A5)
$$

Eigenvalues (λ) are given as solutions of the following equation:

$$
(r_1 - m - \lambda)(r_2 - m - \lambda)(-d - \lambda) = 0. \quad (A6)
$$

The condition for this equilibrium to be locally stable is given by that for all negative solutions λ; that is, $m/r_1 > 1$.

Literature Cited

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

Caswell, H. 1978. Predator mediated coexistence: a non-equilibrium model. American Naturalist 112:127–154.

Comins, H. N., and M. P. Hassell. 1996. Persistence of

multispecies host-parasitoid interactions in spatially distributed models with local dispersal. Journal of Theoretical Biology 183:19–28.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science (Washington, D.C.) 199:1302–1310.

Connell, S. D. 2000. Is there safety-in-numbers for prey? Oikos 88:527–532.

Cramer, N. F., and R. M. May. 1972. Interspecific competition, predation and species diversity: a comment. Journal of Theoretical Biology 34:289–293.

Crowley, P. H. 1979. Predator-mediated coexistence: an equilibrium interpretation. Journal of Theoretical Biology 80:129–144.

Fujii, K. 1977. Complexity-stability relationship of two-prey-one-predator species system model: local and global stability. Journal of Theoretical Biology 69: 613–623.

Gleeson, S. K., and D. S. Wilson. 1986. Equilibrium diet: optimal foraging and prey coexistence. Oikos 46: 139–144.

Hanski, I. A., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, Calif.

Hassell, M. P., and R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. Journal of Animal Ecology 43:567–594.

Hastings, A. 1990. Spatial heterogeneity and ecological models. Ecology 71:426–428.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197–229.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. American Naturalist 144:954–977.

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

Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104: 501–528.

Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. American Naturalist 147:784–812.

Levin, S., and D. Pimentel. 1981. Selection of intermediate rates of increase in parasite-host systems. American Naturalist 117:308–315.

Levin, S. A., and R. T. Paine. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences of the USA 71: 2744–2747.

Lewis, M. A. 1997. Variability, patchiness, and jump dispersal in the spread of an invading population. Pages 46–69 in D. Tilman and P. Kareiva, eds. Spatial ecology. Princeton University Press, Princeton, N.J.

Lloyd, M. 1967. Mean crowding. Journal of Animal Ecology 36:1–30.

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. American Naturalist 112:23–39.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton University Press, Princeton, N.J.

Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. Journal of Animal Ecology 61:37–40.

Pacala, S. W., and M. J. Crawley. 1992. Herbivores and plant diversity. American Naturalist 140:243–260.

Pacala, S. W., and S. A. Levin. 1997. Biologically generated spatial pattern and the coexistence of competing species. Pages 204–232 in D. Tilman and P. Kareiva, eds. Spatial ecology. Princeton University Press, Princeton, N.J.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Richards, S. A., W. G. Wilson, and J. E. S. Socolar. 1999. Selection for intermediate mortality and reproduction rates in a spatially structured population. Proceedings of the Royal Society of London B, Biological Sciences 266:2383–2388.

Sato, K., H. Matsuda, and A. Sakai. 1994. Pathogen invasion and host extinction in lattice structured populations. Journal of Mathematical Biology 32:251–268.

Shorrocks, B., W. Atkinson, and P. Charlesworth. 1979. Competition on a divided and ephemeral resource. Journal of Animal Ecology 48:899–908.

Tansky, M. 1978. Switching effect in prey-predator system. Journal of Theoretical Biology 70:263–271.

Teramoto, E., K. Kawasaki, and N. Shigesada. 1979. Switching effect of predation on competitive prey species. Journal of Theoretical Biology 79:305–315.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.

———. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75:2–16.

Tilman, D., and P. Kareiva. 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, Princeton, N.J.

Tilman, D., and S. Pacala. 1993. The maintenance of species richness in plant communities. Pages 13–25 in R. E. Ricklefs and D. Schluter, eds. Species diversity in ecological communities. University of Chicago Press, Chicago.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371:65–66.

Vulinec, K. 1990. Collective security: aggregation by insects as a defense. Pages 251–288 *in* D. L. Evans and J. O. Schmidt, eds. Insect defenses: adaptive mechanisms and strategies of prey and predators. State University of New York Press, Albany.

Associate Editor: Mathew A. Leibold