

Running from Trouble: Long-Distance Dispersal and the Competitive Coexistence of Inferior Species

E. E. Holmes^{1,*} and H. B. Wilson^{2,†}

1. Zoology Department, University of Washington, Seattle, Washington 98195-1800;

2. Department of Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY, United Kingdom

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Colonization-competition trade-offs have long been heralded as a mechanism for promoting the competitive coexistence of species in patchy environments (Hutchinson 1951; Skellam 1951; Horn and MacArthur 1971; Levins and Culver 1971). In short, this mechanism argues that species that are inferior competitors in local patches can coexist with superior species by having a higher dispersal rate. Empirical evidence for colonization-competition trade-offs comes from fungi communities (Armstrong 1976), species of *Daphnia* (Hanski and Ranta 1983), chalk grasslands of England and Europe (Grubb 1986), fly communities (Hanski 1990), and grasslands of Minnesota (Tilman 1994). These trade-offs also have well-established theoretical foundations from over 25 yr of work on competitive coexistence using patch models (e.g., Levins 1970; Levins and Culver 1971; Hastings 1980; Nee and May 1992; Hanski and Zhang 1993; Tilman 1994; Tilman et al. 1994; Comins and Hassell 1996).

When biologically interpreting the colonization-competition trade-off in these patch models, it is natural to infer that it is a theoretical prediction about dispersal distances and competitive coexistence. Certainly many of the models were developed with the idea of an inferior competitor that disperses its offspring widely outside a local patch versus a superior competitor that disperses its

offspring mostly locally. However, the patch models that are normally used to study the colonization-competition trade-off (such as those in Levins and Culver 1971; Hastings 1980; Tilman 1994) are not explicitly spatial, meaning the environment is broken into patches but the patches do not have an explicit spatial location. Thus, dispersal distance has only an implicit meaning in the sense of within- versus between-patch dispersal. These models explore the effect of the numbers of colonists that are sent outside their local patch, not the explicit dispersal distance. In this case, the strict interpretation of the colonization-competition trade-off is that to survive the inferior competitor must send out viable colonists at a sufficiently higher rate than the superior competitor.

What then is the importance of dispersal distance per se in competitive interactions between two species? A number of spatially explicit models have been developed that model competition between species that disperse their offspring different distances (Weiner and Conte 1981; Pacala 1986; Crawley and May 1987; Hobbs and Hobbs 1987; Czaran and Bartha 1989). Although only one of these studies (Pacala 1986) was designed to directly study the effect of dispersal distance, all suggest that the dispersal distance has an effect on the ability of an inferior competitor to coexist. Using detailed models of plant population dynamics, Pacala (1986) showed that localized dispersal caused an aggregated spatial distribution and a decreased equilibrium density. These changes in turn enhanced the ability of an equal or inferior competitor to invade. When two species were equal competitors, the species with a longer dispersal distance could invade a monoculture of the species with the shorter dispersal distance but not vice versa. These latter results came from a simulation study for one set of life-history parameters and only looked at invasion success, but they suggest strongly that differential dispersal distances affect the ability of species to coexist. Crawley and May (1987) looked directly at coexistence conditions using a spatially explicit patch model of competition between an annual and a perennial in which the perennial was a superior competitor for space but the annual was both a more prolific and longer distance colonizer. As in Pacala's study, localized dispersal by the superior species caused it

* E-mail: eli@zoology.washington.edu.

† E-mail: h.b.wilson@ic.ac.uk.

to clump and lowered its equilibrium density. This in turn enhanced the coexistence of the inferior species. Czaran and Bartha (1989) developed a model for the dynamics of 11 weedy plant species and compared simulations assuming localized versus global dispersal. They found that the inclusion of localized dispersal greatly changed the transient densities. A qualitatively similar result was seen by Dytham (1994) in a study of the effect of habitat destruction on the densities of two locally dispersing competitors. Dytham showed that local dispersal significantly changed the densities and persistence thresholds of the two species.

A consistent observation in these studies is that localized dispersal causes a clumped spatial distribution and a lower overall density and that these effects can in turn benefit a competing species. However, each of the models is very different and many of the results are based on simulations with which only limited parameter space exploration is possible. It is not clear whether a large difference between the dispersal distances of two competitors fundamentally changes coexistence criteria as opposed to simply lengthening the time to reach equilibrium, quantitatively but not qualitatively changing coexistence criteria, or causing changes only on account of interactions with other attributes of the model such as gap or patch size. In order to further a basic understanding of the importance of dispersal distance, we return to the simplified patch occupancy models that have often been used to study the colonization-competition trade-off. However, we add explicit spatial location and explicit distances between patches. Specifically, we use cellular automaton analogues of patch occupancy models. Similar cellular automaton models have been used recently to explore the spatial population dynamics of competing plant species and other sedentary species (Karlson and Jackson 1981; Crawley and May 1987; Inghe 1989; Rees and Long 1992; Silvertown et al. 1992; Colasanti and Grime 1993; Halley et al. 1994; Molofsky 1994).

We study two models of two-species hierarchical competition. When the competitors disperse their offspring equal distances, both models require a trade-off between colonization and competitive ability in order for the two species to coexist. We specifically address whether this colonization-competition trade-off is required when the inferior competitor disperses its offspring over a much wider area than the superior competitor. The colonization-competition trade-off is a fundamental aspect of many simple patch models of competition. Whether wider dispersal by the inferior competitor can overcome this requirement is in essence a litmus test of the power of long-distance dispersal. We study the criteria for coexistence at equilibrium and do not explore whether the steady states are static, cyclic, or chaotic. Throughout, we

explore the benefit of long-distance dispersal only. Some studies have shown that localized dispersal can enhance coexistence by segregating competitors (Pacala 1986). However, this is not explored for the simple reason that for the types of cellular automaton models used here, localized dispersal either does not change the equilibrium state or uniformly makes equilibrium coexistence more difficult (Durrett 1991; Durrett and Moller 1991; Durrett and Swindle 1991).

Hierarchical Competition

We first consider competition in which one species is a superior competitor for space and can both exclude the inferior competitor from a site and remove it by colonizing on top of it. When both species disperse globally, we have the following patch occupancy model (Levins and Culver 1971; Hastings 1980; Nee and May 1992) for the fraction of sites occupied by the superior, S , and inferior competitor, I :

$$\frac{dS}{dt} = c_s S(1 - S) - \delta S$$

(1)

and

$$\frac{dI}{dt} = c_i I(1 - S - I) - \delta I - c_s SI,$$

where c_s and c_i are the colonization rates of each species (superior and inferior, respectively), and δ is the local extinction rate. We assume for clarity of presentation that the extinction rates of the superior and inferior species are equal. The coexistence criterion for equation (1) is (Hastings 1980):

$$c_i > c_s \left(\frac{c_s}{\delta} \right).$$

(2)

Since the superior's colonization rate must be greater than its death rate to persist, c_i must be greater than c_s . This is the colonization-competition trade-off (fig. 1A).

To study the advantage conferred by long-distance dispersal, we consider a cellular automaton analogue of the patch occupancy model (see Mollison and Kuulasmaa 1985 or Durrett and Levin 1994 for an introduction to ecologically oriented cellular automaton models). The habitat is considered to be an infinite square grid of sites. Each site can contain only one individual and has a set of four immediate neighbors. The superior competitor can colonize only locally onto its immediately neighboring four sites while the inferior competitor disperses its offspring over the entire grid. Thus, in this model, the inferior species has an infinitely longer dispersal distance than the superior species.

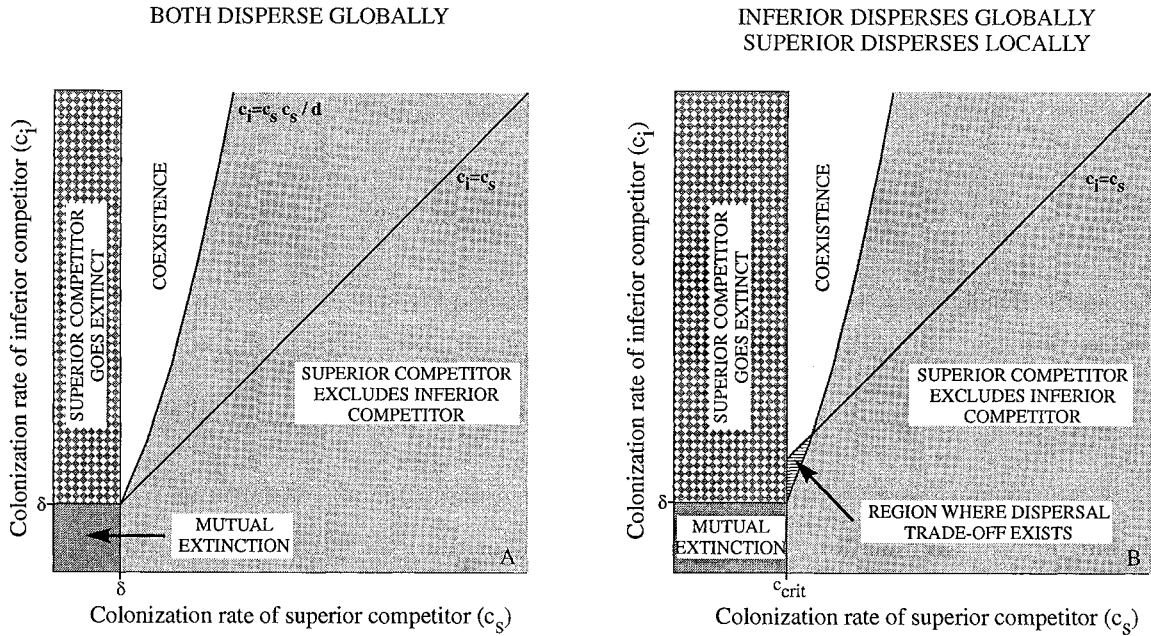


Figure 1: Hierarchical competition with exclusion and mortality. A, Patch occupancy model. In this model, both species disperse equally and globally. The inferior competitor must have a colonization advantage to coexist with the superior competitor. This is the colonization-competition trade-off. B, Cellular automaton model. In this model, the inferior competitor colonizes globally and the superior competitor colonizes locally. When the colonization rate of the superior species is small (and the observed fraction of occupied sites is correspondingly small), a dispersal-competition trade-off exists. In this region, long-distance dispersal of offspring allows an inferior competitor with a small colonization disadvantage to coexist with the superior species.

The model can be described explicitly as below. At each, very small, time step, sites make transitions according to the following probabilities. (1) With probability $c_s dt$, the superior competitor sends out a colonist to a randomly chosen neighboring site. If the site is empty or occupied by the inferior competitor, the colonist establishes. (2) With probability $c_i dt$, the inferior competitor sends out a colonist. The colonist has an equal probability of landing on any site in the grid. If it lands on an empty site, it establishes; otherwise it dies. (3) The inferior and superior competitors die with probability δdt .

Using a mean field argument described in the appendix, we show that the coexistence criterion for the inferior competitor is:

$$c_i > \frac{\delta S^*}{(1 - S^*)^2} + \frac{\delta}{1 - S^*}, \quad (3)$$

where S^* is the equilibrium fraction of sites occupied by superior competitor in the cellular automaton model. There is no equation for S^* in terms of c_s . However, information about the relationship between S^* and c_s can be used to determine the qualitative shape of the coexistence criterion.

When the superior competitor is rare ($S^* \approx 0$), it will persist only if its colonization rate, c_s , is greater than its

death rate, δ , by some margin (Durrett 1991; Mollison and Levin 1995). This margin compensates for intraspecific competition due to local colonization. From simulations, the minimum colonization rate is approximately $c_s = 1.65\delta$ when colonists disperse to the nearest four neighbors only (Durrett 1991; Mollison and Lewis 1995). At the same time, when the superior competitor is rare, the minimum colonization rate for the inferior competitor is simply $c_i = \delta$. Thus, when the superior competitor is rare, the inferior competitor can have a lower colonization rate than the superior competitor yet still persist (fig. 1B). In this case, the inferior competitor can coexist by virtue of its long-distance dispersal.

When the superior competitor is common, we can use a simple argument to show that c_i must be greater than c_s . When the superior competitor occupies most of the space, any inferior site will be surrounded by approximately four superior neighbors. The rate that the superior competitor colonizes onto inferior sites is then approximately $4c_s I$. The coexistence criterion for the inferior species is $c_i(1 - S^*) > 4c_s + \delta$. Since $0 \leq S^* \leq 1$, c_i must be greater than c_s (fig. 1B). In general, c_i must be greater than c_s when the average number of superior neighbors per inferior site is > 1 . Thus, a colonization-competition trade-off is required when the superior competitor is common.

The results from the cellular automaton model are related to results from studies on aggregation and coexistence. In the cellular automaton model, the offspring of the superior species are dispersed near the parent. When the superior competitor is rare, this type of local colonization produces an aggregated colonization distribution. That is, the vast majority of patches receive no colonists, and a few patches (i.e., the neighboring patches) receive many colonists. When the superior species is common, however, most patches receive a similar number of colonists so that there is little aggregation. Aggregation as a mechanism for coexistence has been studied by a number of authors (e.g., Atkinson and Shorrocks 1981; Ives and May 1985; Green 1986; Shorrocks 1990; Dytham and Shorrocks 1992, 1995). The results of these models indicate that when intraspecific aggregation is greater than interspecific aggregation, coexistence of superior and inferior competitors is facilitated (Ives 1988; McPeck and Holt 1992).

Hierarchical Competition for Space Alone

In the previous model, the superior competitor causes mortality of the inferior competitor. We now analyze the case when the two species compete only for space. Here, the inferior species is an annual and is not killed by the superior perennial species; it simply cannot colonize sites occupied by the superior species. An example of this type of model is Crawley and May's (1987) spatial model of a competitively inferior annual plant, which spreads its seeds widely, versus a competitively superior perennial plant, which spreads ramets only locally.

We first consider the case when both species disperse globally and randomly. This is represented by a patch occupancy model:

$$S_{t+1} = [1 - (1 - \delta_s)S_t](1 - \exp(-c_s S_t)) + (1 - \delta_s)S_t, \quad (4)$$

and

$$I_{t+1} = (1 - S_{t+1})(1 - \exp(-c_i I_t)).$$

The $1 - \exp(-x)$ term is the fraction of sites that receive at least one colonist. The model is written with discrete time that allows competition to occur only during the colonization phase. The condition for coexistence for model (4) is:

$$c_i > \frac{1}{1 - \hat{S}}. \quad (5)$$

It can be shown that the colonization-competition trade-off is necessary for coexistence by observing from equation (4) that $\hat{S} > 1 - \delta_s/c_s$. This means that at the point when coexistence is just possible (when $c_i = 1/[1 - \hat{S}]$),

the production of colonists by the inferior competitor must be greater than that of the superior competitor (fig. 2A). The death rates of the two species are different, thus the colonization-competition trade-off is stated in terms of the lifetime production of colonists, c_i/δ_i and c_s/δ_s , where $\delta_i = 1$.

To look at the effect of long-distance dispersal, we consider a cellular automaton analogue of this model, in which the inferior competitor disperses globally and the superior competitor disperses locally (see also Durrett and Levin 1994). Durrett and Schinazi (1993) have shown that the coexistence criterion is

$$c_i > \frac{1}{1 - S^*}, \quad (6)$$

where S^* is the equilibrium fraction of sites occupied by the superior species in the cellular automaton model. This result is the same as that derived by Crawley and May (1987) via a different analysis.

Because there is not an equation for S^* , it is not possible to write down an equation for the coexistence criterion as a function of c_i and c_s . However, we can qualitatively characterize the coexistence criterion (fig. 2B). As discussed for the previous cellular automaton model, c_s must be greater than δ_s by some margin to compensate for intraspecific competition due to local dispersal, $c_s/\delta \geq c_{crit}/\delta = 1 + m$. When c_s is close to c_{crit} , the superior species is rare and $S^* \approx 0$. At this point, the criterion for coexistence of the inferior competitor is $c_i > 1$. An inferior competitor with c_i , such that $1 < c_i < 1 + m$ has a colonization rate that is lower than that of the superior species, but it still can coexist. Thus, a higher lifetime colonization rate, c/δ , is not strictly necessary when the superior species is rare.

When the superior competitor is abundant, we note that as the colonization rate of the superior species increases, the fraction of space that it occupies approaches 1. We observe from simulations that

empty space in global model

empty space in cellular automaton model

$$= \frac{1 - \hat{S}}{1 - S^*} \rightarrow 1, \quad \text{as } c_s/\delta_s \rightarrow \infty.$$

From equation (4), $\hat{S} \approx 1 - \delta_s \exp(-c_s)$ when \hat{S} is very close to 1. If we substitute $1 - \delta_s \exp(-c_s)$ into equation (6), then we see that c_i/S_i must be greater than c_s/S_s (fig. 2B). When the superior competitor is common, the inferior competitor must have a higher colonization rate.

Time to Extinction and Noninstantaneous Exclusion

In our discussion of coexistence conditions, we focused on the equilibrium condition for coexistence. However,

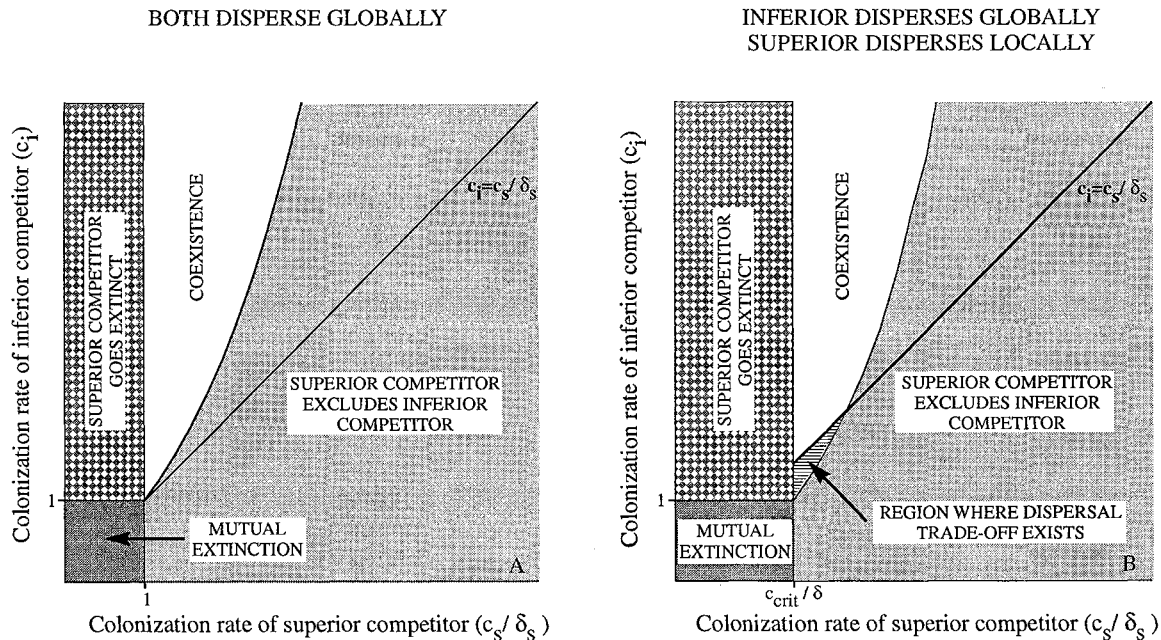


Figure 2: Hierarchical competition model with exclusion only. In this model, the superior species does not cause direct mortality of the annual but merely preempts colonization sites. *A*, The patch-occupancy model where both species disperse globally. *B*, The cellular automaton model in which the superior competitor disperses locally. The coexistence regions are similar to those for the cellular automaton model in figure 1*B*.

one can well imagine conditions under which this equilibrium is approached so slowly that the two species coexist for indefinite ecological time even though the inferior competitor is doomed to extinction. Here, we give a qualitative feel for how quickly an inferior species will be excluded for the first hierarchical competition model (eq. [1]).

If the superior competitor invades a monoculture of the inferior competitor, the superior species spreads outward at a constant velocity (Cox and Durrett 1988) and eliminates the inferior species in its wake. From simulations, the velocity is approximately $0.83c_s\sqrt{2}$ when $\delta = 0$ (the superior competitor is immortal) and decreases steadily to 0 as δ increases (Mollison and Kuulasmaa 1985; Mollison 1991). Obviously, the time until the inferior species is eliminated will depend on the size of the habitat over which the superior species must spread. The inferior species will persist for some period in the wake of the superior species. Via a mass-action argument (see the appendix), the rate of change of the inferior species can be approximated by the function

$$\frac{dI}{dt} = -\frac{\delta}{1-S^*}S^*I - \delta S^*I + c_iI(1-I-S^*). \quad (7)$$

The upper bound on the time for I to halve is $\ln(2)/[\delta + S^*\delta/(1-S^*) + c_iS^* - c_i]$. If the inferior species

is almost but not quite able to persist at equilibrium, meaning that $c_i \approx \delta + S^*\delta/(1-S^*) + c_iS^*$, then it will take a long time for the inferior species to go extinct. Notice that regardless of whether the equilibrium state is relevant on an ecological timescale, the knowledge of the equilibrium coexistence criterion gives us information to estimate extinction times.

The opposite case, when the inferior competitor invades a monoculture of the superior competitor, brings up an interesting issue concerning the value of long-distance dispersal. If it is stipulated that the inferior species is not able to coexist at equilibrium, then the inferior species cannot invade the superior species even if the superior species is rare and there is ample empty space. However, intuitively, if there is an abundance of empty space, an inferior competitor might be able to invade that space, at least temporarily. In this case, the inferior's long-distance dispersal is its downfall. Since it disperses its offspring globally, it does not stay in the empty areas but disperses out into areas with a high density of the superior competitor. In this situation, local dispersal can allow an inferior species to temporarily persist in an empty area—until the superior species spreads there. A similar type of mechanism allows two locally dispersing species to coexist in spatially explicit metapopulation models in which large portions of habitat are periodically

destroyed (Dytham 1994). Local dispersal can enhance diversity by allowing species to remain longer in local refugia.

In the same vein, it is possible to consider the consequences of a noninstantaneous time to exclusion within an individual patch. Previously we assumed that the within-patch dynamics are very quick (relatively instantaneous) compared with the colonization and extinction processes. We now relax this assumption and assume that the superior competitor takes a fixed amount of time, τ , to take over a patch already colonized by the inferior. The superior species is unaffected, but the rate of change of the inferior species is now approximated by

$$\frac{dI}{dt} = -\delta I_i - C_s S_{i-\tau} I_{i-\tau} \exp(-\delta\tau) + c_i I_i (1 - I_i - S_i), \quad (8)$$

where the second term is the loss of patches due to colonization by the superior competitor at time τ in the past (multiplied by the probability that they have not already gone extinct). At equilibrium, C_s can be approximated by $\delta/(1 - S^*)$ (see the appendix), which gives the coexistence criterion:

$$c_i > \frac{\delta S^* \exp(-\delta\tau)}{(1 - S^*)^2} + \frac{\delta}{1 - S^*}. \quad (9)$$

This is the same as criterion (3) except that the first term (loss of sites due to colonization by the superior competitor) is multiplied by $\exp(-\delta\tau)$. When $\tau \rightarrow 0$ and exclusion is instantaneous, then the original criterion is obtained. When $\tau \rightarrow \infty$, so that the superior competitor never excludes the inferior species, then this term disappears. The criterion then becomes qualitatively similar to criterion (6) in the hierarchical model, which did not include mortality due to colonization by the superior species. Between these two extremes, the criterion for coexistence is less strict than criterion (3), and it is easier for the inferior competitor to coexist. However, the conclusions reached earlier remain valid: an inferior competitor can coexist due to long-distance dispersal alone only when the superior competitor is rare.

It is also possible to relax the assumption that the inferior competitor can never colonize a patch occupied by the superior competitor. In particular, one can suppose that the inferior species can invade sites that have just recently been invaded by the superior species. S. W. Pacala and M. Rees (unpublished manuscript) have analyzed this model (with both species dispersing globally) and have shown that in the limit when the colonization rate is very much greater than the death rate, the two species can always coexist. In this case, coexistence of the two species depends on the unlimited availability of colonists of both species, while the models outlined in this note as-

sume that colonization is a limiting process. However, our results still remain valid. When there is an unlimited supply of colonists, then the dominant species will be very common. In this case, long-distance dispersal alone is insufficient to maintain persistence of the inferior competitor. Rather, another mechanism must act (in the case of Pacala and Rees, it is an early successional niche) in order for the two species to coexist.

Discussion

In this note, we studied long-distance dispersal as mechanism for the coexistence of species and particularly as a mechanism to overcome the requirement for a colonization-competition trade-off. Our analysis makes some general predictions concerning the dispersal traits of coexisting hierarchical competitors. When the superior competitor is common, the inferior competitor should produce more colonists or their offspring should be better able to colonize empty sites. One should not find inferior competitors with only long-distance dispersal and without a higher colonization rate. If, on the other hand, the superior species is rare, it is possible for a long-distance disperser, which is both an inferior competitor and an inferior reproducer, to coexist. The region of parameter space where this is possible may, however, be very small. The size of this region depends on the details of the intraspecific competition experienced by the superior competitor.

Possible examples of such trends in real systems are difficult to find as there is relatively little data on dispersal distances and measures of competitiveness. However, one possible example comes from extensive work on colonization-competition trade-offs in prairie grasslands. The superior competitors are not extremely rare in this example (Tilman and Wedin 1991), and the theory predicts that poor competitors must send out more colonists during their expected lifespan than superior competitors—even if those colonists are dispersed over longer distances. Tilman and Wedin (1991) measured competitive ability and viable seed production of five prairie grasses. Worse competitors consistently had a higher seed set, with one exception. The one exception was *Agropyron repens*. This species was a poor competitor with low seed output. The low seed output was not compensated by small seeds that might be associated with long-distance dispersal; in fact, *Agropyron* had the largest seeds. Instead, *Agropyron* had the highest investment into rhizomes; in this case, low seed set appeared to be compensated for by high vegetative colonization.

Another example may be sand dune annuals. A negative relationship has been reported between dispersal ability and competitive ability; larger seeded sand dune annuals tend to be better competitors than smaller

seeded species (Mack and Harper 1977; Rees 1995). Although there are few data on dispersal distances, these seeds are dispersed passively, and small, light seeds may reasonably disperse farther than larger, heavier seeds. The dominant competitors tend to be rare, suggesting that this is a system in which long-distance dispersal may allow inferior competitors to coexist without producing a greater number of colonists. However, as in the prairie grassland example, we do not see this sort of trade-off. The inferior competitors (with small seeds) also produce many more seeds. A final example may be plants that produce winged seeds (e.g., *Fraxinus excelsior* and *Acer pseudoplatanus*). If long-distance dispersal is a significant advantage, one might see lower seed production in these plants. However, data indicate (Grime 1979) that these winged plants also produce large numbers of seeds.

Neither of these three examples show an obvious dispersal distance–competition trade-off (a parameter region where long-distance dispersal overcomes both a competitive and colonization disadvantage). Our study might overlap the existence of a dispersal distance–competition trade-off because we considered only two-species competition. In this case, the theory predicts that long-distance dispersal can compensate for a lower colonization rate when the dominant species is rare. In a multispecies environment, it is unlikely that all other species will be rare. In this environment, therefore, long-distance dispersal may be less of an advantage and coexistence may simply depend on producing more seeds.

Clearly, many aspects of natural communities play a part in determining the relevance of simple theoretical predictions, such as trade-offs between colonization, competition, and dispersal distance. Simple spatial models are caricatures of competition in nature, yet understanding their behavior helps clarify the spatial mechanisms that drive the behavior of more complex and realistic spatial systems.

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APPENDIX

Coexistence Criterion for the Cellular Automaton

Below we derive the coexistence criterion for the cellular automaton version of model (1). Because the inferior competitor disperses globally, we can use a mean field ar-

gument to determine its colonization criterion. We specify the order of events during each time step as: inferior sends out seed everywhere; superior spreads; superior dies; inferior dies; inferior's seeds emerge in the empty spaces. Since the time step is very, very short, the ordering is not critical.

The fraction of sites that are occupied by the inferior species at time $t + dt$ is the number of inferior sites at time t that neither die nor are overtaken by the superior species plus the fraction of sites that are empty and received at least one seed. Thus,

$$I_{t+dt} = (1 - S^*)(1 - \exp(-c_i dt I_t)) + \exp(-c_i dt I_t) \times \left[I_t - \delta dt I_t - (1 - \delta dt) I_t \frac{\delta dt S^*}{1 - S^*} \right] = \phi(I_t). \quad (\text{A1})$$

The parameters are: c_i , the colonization rate; δ , the death rate; I_t , the fraction of inferior sites at time t ; and S^* , the equilibrium fraction of superior sites. The two terms in equation (A1) are (1) the fraction of sites that are not occupied by the superior multiplied by the probability of receiving a seed from the inferior species—this is the rate that inferior sites colonize empty sites; and (2) a site may also be occupied by the inferior if it was occupied by the inferior species in the previous time step and neither died nor was overtaken by a superior colonist. Thus the second term is the fraction of sites that were occupied in the previous time step minus those that died minus those that lived but were overtaken by superior colonists. Since the superior species is at equilibrium, the fraction of sites it colonizes is equal to the fraction that die, δS^* . These colonists occur among the available empty sites. Thus the probability that an inferior site is overtaken is $\delta S^*/(1 - S^*)$. The whole second term is multiplied by the probability that the site did not receive a seed so that sites that receive seeds and remain occupied are not counted twice.

If the inferior species can coexist, then there exists some \hat{I} such that $\hat{I} = \phi(\hat{I})$. To determine the conditions under which such a solution exists, note the following:

$$\begin{aligned} \phi'(x) &= c_i dt (1 - S^*) \exp(-c_i dt x) \\ &\quad + b \exp(-c_i dt x) - c_i dt x b \exp(-c_i dt x) \\ &= c_i dt \exp(-c_i dt x) [(1 - S^*) - xb] \\ &\quad + b \exp(-c_i dt x), \end{aligned} \quad (\text{A2})$$

where $b = 1 - \delta dt - (1 - \delta dt) \delta dt S^*/(1 - S^*)$. Note that $\phi'(\hat{I}) > 0$, since $\hat{I} < (1 - S^*)$ and $b < 1$. Since dt is small, $b > 0$. Also,

$$\begin{aligned} \phi''(x) &= -c_i^2 dt^2 \exp(-c_i dt x) [(1 - S^*) - xb] \\ &\quad - 2c_i dt b \exp(-c_i dt x), \end{aligned} \quad (\text{A3})$$

and $\phi''(\hat{I}) < 0$. Thus, $\phi(x)$ is strictly increasing and strictly concave. When $\phi(x)$ has these features, a solution to $\phi(x) = x$, where $0 < x < 1$, exists if and only if $\phi'(0) > 1$ (Durrett and Lewis 1994). Assuming dt is small so that $\exp(-c_i dt x) \approx 1$ and assuming $x \approx 0$ (i.e., the limiting case when the inferior competitor is very rare), the coexistence criterion for the inferior species is

$$c_i dt(1 - S^*) + 1 - \delta dt - (1 - \delta dt)\delta dt S^*/(1 - S^*) > 1. \quad (\text{A4})$$

After dropping terms with dt^2 and dividing by dt , this becomes

$$c_i > \frac{\delta}{1 - S^*} + \frac{\delta S^*}{(1 - S^*)^2}. \quad (\text{A5})$$

Literature Cited

- Armstrong, R. A. 1976. Fugitive species: experiments with fungi and some theoretical considerations. *Ecology* 57:953–963.
- Atkinson, W. D., and B. Shorrocks. 1981. Competition on a divided resource. *Journal of Animal Ecology* 50:461–471.
- Colasanti, R. L., and J. P. Grime. 1993. Resource dynamics and vegetation processes: a deterministic model using two-dimensional cellular automata. *Functional Ecology* 7:169–176.
- 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.
- Cox, J. T., and R. Durrett. 1988. Limit theorems for the spread of epidemics and forest fires. *Stochastic Processes and Their Applications* 30:171–191.
- Crawley, M. J., and R. M. May. 1987. Population dynamics and plant community structure: competition between annuals and perennials. *Journal of Theoretical Biology* 125:475–489.
- Czaran, T., and S. Bartha. 1989. The effect of spatial pattern on community dynamics: a comparison of simulated and field data. *Vegetatio* 83:229–239.
- Durrett, R. 1991. Stochastic models of growth and competition. Pages 1049–1056 in I. Satake, ed. *Proceedings of the International Congress of Mathematicians, Kyoto 1990*. Springer, Tokyo.
- Durrett, R., and S. Levin. 1994. Stochastic spatial models: a user's guide to ecological applications. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 343:329–350.
- Durrett, R., and A. M. Moller. 1991. Complete convergence theorem for a competition model. *Probability Theory and Related Fields* 88:121–136.
- Durrett, R., and R. Schinazi. 1993. Asymptotic critical value for a competition model. *Annals of Applied Probability* 3:1047–1066.
- Durrett, R., and G. Swindle. 1991. Are there bushes in a forest? *Stochastic Processes and Their Applications* 37:19–31.
- Dytham, C. 1994. Habitat destruction and competitive coexistence: a cellular model. *Journal of Animal Ecology* 63:145–146.
- Dytham, C., and B. Shorrocks. 1992. Selection, patches and genetic variation: a cellular automaton modelling *Drosophila* populations. *Evolutionary Ecology* 6:342–351.
- . 1995. Aggregation and the maintenance of genetic diversity: an individual-based cellular model. *Evolutionary Ecology* 9:508–519.
- Green, R. F. 1986. Does aggregation prevent competitive exclusion? a response to Atkinson and Shorrocks. *American Naturalist* 128:301–304.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. Wiley, Chichester.
- Grubb, P. J. 1986. Problems posed by sparse and patchily distributed species in species-rich plant communities. Pages 207–226 in J. Diamond and T. Case, eds. *Community ecology*. Harper & Row, New York.
- Halley, J. M., H. N. Comins, J. H. Lawton, and M. P. Hassell. 1994. Competition, succession and pattern in fungal communities: towards a cellular automaton model. *Oikos* 70:435–442.
- Hanski, I. 1990. Dung and carrion insects. Pages 127–145 in B. Shorrocks and I. R. Swingland, eds. *Living in a patchy environment*. Oxford University Press, Oxford.
- Hanski, I., and E. Ranta. 1983. Coexistence in a patchy environment—three species of *Daphnia* in rock pools. *Journal of Animal Ecology* 52:263–279.
- Hanski, I., and D. Y. Zhang. 1993. Migration, metapopulation dynamics and fugitive coexistence. *Journal of Theoretical Biology* 163:491–504.
- Hastings, A. 1980. Disturbance, coexistence, history and competition for space. *Theoretical Population Biology* 18:363–373.
- Hobbs, R. J., and V. J. Hobbs. 1987. Gophers and grassland: a model of vegetation response to patchy soil disturbance. *Vegetatio* 69:141–146.
- Horn, H. S., and R. H. MacArthur. 1971. Competition among fugitive species in a harlequin environment. *Ecology* 53:749–752.
- Hutchinson, G. E. 1951. Copepodology for the ornithologist. *Ecology* 32:571–577.
- Inghe, O. 1989. Genet and ramet survivorship under dif-

- ferent mortality regimes—a cellular automaton model. *Journal of Theoretical Biology* 138:257–270.
- Ives, A. R. 1988. Covariance, coexistence and the population dynamics of two competitors using a patchy resource. *Journal of Theoretical Biology* 133:345–361.
- 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.
- Karlsou, R. H., and J. B. C. Jackson. 1981. Competitive networks and community structure: a simulation study. *Ecology* 62:670–678.
- Levins, R. 1970. Extinction. Pages 75–107 in M. Gerstenhaber, ed. *Some mathematical problems in biology*. American Mathematical Society, Providence, R.I.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the USA* 68:1246–1248.
- Mack, R. N., and J. L. Harper. 1977. Intereference in dune annuals: spatial pattern and neighbourhood effects. *Journal of Ecology* 65:345–363.
- McPeck, A. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. *American Naturalist* 140:1010–1027.
- Mollison, D. 1991. Dependence of epidemic and population velocities on basic parameters. *Mathematical Biosciences* 107:255–287.
- Mollison, D., and K. Kuulasmaa. 1985. Spatial epidemic models: theory and simulations. Pages 291–309 in P. J. Bacon, ed. *Population dynamics of rabies in wildlife*. Academic Press, London.
- Mollison, D., and S. A. Levin. 1995. Spatial dynamics of parasitism. Pages 384–398 in B. T. Grenfell and A. P. Dobson, eds. *Ecology of infectious diseases in natural populations*. Cambridge University Press, Cambridge.
- Molofsky, J. 1994. Population dynamics and pattern-formation in theoretical populations. *Ecology* 75:30–39.
- 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. 1986. Neighborhood models of plant population dynamics. 2. Multi-species models of annuals. *Theoretical Population Biology* 29:262–292.
- Rees, M. 1995. Community structure in sand dune annuals—is seed weight a key quantity? *Journal of Ecology* 83:857–863.
- Rees, M., and M. J. Long. 1992. Germination biology and the ecology of annual plants. *American Naturalist* 139:484–508.
- Shorrocks, B. 1990. Competition and selection in a patchy and ephemeral habitat: the implications for insect life cycles. Pages 215–228 in F. Gilbert, ed. *Insect life cycles*. Springer, London.
- Silvertown, J., S. Holtier, J. Johnson, and P. Dale. 1992. Cellular automaton models of the competition for space—the effect of pattern on process. *Journal of Ecology* 80:527–534.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* 38:196–218.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Tilman, D., and D. Wedin. 1991. Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology* 72:685–700.
- Tilman, D., R. M. May, D. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature (London)* 371:65–66.
- Weiner, J., and P. T. Conte. 1981. Dispersal and neighborhood effects in an annual plant competition model. *Ecological Modelling* 13:131–147.