

Resource-Dependent Dispersal and the Speed of Biological Invasions

Greg Dwyer^{1,*} and William F. Morris^{2,†}

1. Department of Ecology and Evolution, University of Chicago, Chicago, Illinois 60637;

2. Department of Biology, Duke University, Box 90338, Durham, North Carolina 27708

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ABSTRACT: Many mobile organisms exhibit resource-dependent movement in which movement rates adjust to changes in local resource densities through changes in either the probability of moving or the distance moved. Such changes may have important consequences for invasions because reductions in resources behind an invasion front may cause higher dispersal while simultaneously reducing population growth behind the front and thus lowering the number of dispersers. Intuiting how the interplay between population growth and dispersal affects invasions is difficult without mathematical models, yet most models assume dispersal rates are constant. Here we present spatial-spread models that allow for consumer-resource interactions and resource-dependent dispersal. Our results show that when resources affect the probability of dispersal, then the invasion dynamics are no different than if resources did not affect dispersal. When resources instead affect the distance dispersed, however, the invasion dynamics are strongly affected by the strength of the consumer-resource interaction, and population cycles behind the wave front lead to fluctuating rates of spread. Our results suggest that for actively dispersing invaders, invasion dynamics can be determined by species interactions. More practically, our work suggests that reducing invader densities behind the front may be a useful method of slowing an invader's rate of spread.

Keywords: biological invasion, nonindigenous species, integrodifference equations, resource-dependent dispersal, spatial spread.

Many mobile organisms increase their feeding efficiency through resource-dependent movement in which foraging movements are adjusted in response to local resource den-

sities (Sutherland et al. 2002). Two important ways by which resources may affect movement are first by affecting the probability of moving, typically such that movement is more likely when resources are lower. For example, insects that disperse by ballooning often choose whether to balloon on the basis of local resource availability (Hunter and Lechowicz 1992; Rhainds et al. 2002), but the distance that they disperse is determined only by wind speed and other features of the physical environment. Second, resources may affect the distance moved. For example, in area-restricted search, consumers in areas with relatively high resources move less frequently, turn more frequently, and/or reduce their speed of movement. Such consumers therefore tend to disperse shorter distances in areas where resources are at higher density (Kareiva and Odell 1987). This behavior has been observed in diverse animal taxa, including nematodes, insects and other arthropods, fish, birds, mammals, and even bacteria and protists (for partial introductions to the vast literature on this subject, see Segel 1977; Kareiva and Odell 1987; Morris and Kareiva 1991; Keasar et al. 1996; Turchin 1998; Fryxell et al. 2004).

Intuitively, one might expect that these widespread behaviors would influence the rate at which exotic species invade new territory. At an invasion front, individuals encountering higher resources should disperse less frequently and not as far, while those behind the front, experiencing reduced resource concentrations because of their own feeding, should disperse more frequently and farther, bringing more of them to the front, where they can contribute to population spread. Lower resource densities behind the front, however, might also restrict population growth through either lower birth rates or higher mortality rates, thereby reducing the number of individuals available to disperse toward the front. Intuiting the effects of resource-dependent dispersal on invasions is thus not a trivial task; in fact, it can be difficult to intuit the population-level consequences even of far simpler movement behaviors (Holmes et al. 1994).

One way to deduce the population-level consequences of movement behaviors for invasion dynamics is by using mathematical models (Murray 1991). Indeed, models are

* E-mail: gdwyer@uchicago.edu.

† E-mail: wfmorris@duke.edu.

widely used to analyze invasion data (Lubina and Levin 1988; Clark et al. 1998) and to make inferences about the long-term dynamics of spread from short-term observations of movement (Kot et al. 1996; Dwyer et al. 1998). Surprisingly, however, despite much research on consumer-resource dynamics (Murdoch et al. 2003) and despite the ubiquity of resource-dependent movement (Sutherland et al. 2002), almost all invasion models assume that dispersal rates are unaffected by resources (Morris and Dwyer 1997; Turchin 1998). The population-level implications of consumer-resource interactions and resource-dependent dispersal for invasion dynamics are therefore poorly understood. In this article, we use models to explore how consumer-resource interactions and resource-dependent dispersal together affect invasions. We consider two different models of resource-dependent dispersal, the first with a resource-dependent probability of dispersal and the second with a resource-dependent distribution of dispersal distances. Although most studies of resource-dependent dispersal measure movement behavior over short time intervals, such short-term behaviors are nevertheless likely to lead to effects of resources on dispersal over an entire generation, which in turn may affect long-term population dynamics (Kareiva and Odell 1987). In both models, we therefore incorporate dispersal in terms of the distance moved in a generation. The questions that we ask are, then, what are the consequences of resource-dependent dispersal for the spread of invading consumers, and how do these consequences depend on the details of how resources affect dispersal? As we will show, when resources affect the distribution of dispersal distances, then the population dynamics behind the front can affect the invasion velocity, and invasion speeds can fluctuate. As we describe in the "Discussion," this result may have important implications both for our understanding of spatial spread and for efforts to control the rate of spread of exotic species.

Methods

Our previous modeling work suggested that resource-dependent dispersal would have no effect on species' invasions (Morris and Dwyer 1997). The models that we used, however, followed the vast majority of spatial-spread models in making restrictive assumptions (Fisher 1937; Murray 1991; Turchin 1998). First, most models assume that dispersal is diffusive, which effectively means that dispersal occurs in the form of many short jumps. In the case of simple diffusion, one of the consequences of this assumption is that dispersal distances are normally distributed. For many organisms, however, distributions of dispersal distances are strongly leptokurtic, meaning that there is an excess of long-distance movements (Kot et al.

1996). Second, our previous model and most others have been formulated in continuous time so that reproduction occurs continuously; many invasive species, however, have discrete generations or discrete breeding periods (Andow et al. 1990; Shigesada and Kawasaki 1997). As a result of these two assumptions, organisms in our previous models dispersed only up to the invasion front, where resources were high, and consequently there was no effect of resources on invasion dynamics (Morris and Dwyer 1997). In nature, however, organisms with resource-dependent dispersal may instead make dispersive leaps from behind the front to well in advance of the front. The main conclusion of our previous work, that resource-dependent movement does not affect invasions, may therefore have depended on assumptions that hold for only a small number of species. In the work that we present here, we instead use integrodifference equations, which assume discrete generations, and allow for the possibility of longer-distance dispersal movement events (Kot et al. 1996; Neubert et al. 2000; Wang et al. 2002; Medlock and Kot 2003).

For simplicity, we treat space as a one-dimensional variable on the grounds that qualitative results for one-dimensional models generally also hold for two-dimensional models (Murray 1991). Our models then keep track of the density of a resource $R_t(x)$ and of a consumer $C_t(x)$ as functions of generation t and distance x from where the consumer was introduced. We assume that the effect of the invading consumer is to reduce $R_t(x)$ but that the resource regrows in the consumer's absence. To isolate the effects of resource-dependent consumer dispersal, we assume that the resource is sessile so that only the consumer disperses. Our equation for local resource dynamics is then

$$R_{t+1}(x) = \frac{\rho R_t(x)}{a + R_t(x)} \exp\left[\frac{-sC_t(x)}{(1 + \mu C_t(x))}\right]. \quad (1)$$

Here we assume that in the absence of the consumer, the resource follows Beverton-Holt dynamics (Gurney and Nisbet 1998); ρ is thus the reproductive rate of the resource at low density in the absence of consumers, while a determines how net resource growth is affected by density, again in the absence of consumers. The advantage of the Beverton-Holt model is that it ensures that the resource has stable population dynamics ahead of the advancing front of consumers, thereby eliminating an unnecessary complication. Other discrete-time formulations, such as the Ricker model or the discrete-time logistic (Gurney and Nisbet 1998), do not share this property; preliminary investigations, however, have suggested that substituting either the Ricker model or the discrete-time logistic gives similar results. To describe consumer feeding, we use what

is essentially a host-parasitoid attack function with interference among consumers so that the fraction of resources surviving the consumer is $\exp[-sC_i(x)/(1 + \mu C_i(x))]$. This function describes the fraction of resources that avoid being consumed and that then go on to grow following the Beverton-Holt model.

This host-parasitoid attack function has the advantage that it can be derived directly from first principles of consumer attack rates and handling times (Beddington 1975) such that the parameters μ and s describe features of consumer feeding behavior. Also, the nonspatial version of this model has been studied intensively (Tang and Chen 2002). This is a useful feature because, as we will describe, the dynamics of the nonspatial version have important implications for the results of one of our spatial models. Most important, there is good evidence that a version of the model provides a good description of the population dynamics of at least some real organisms (Turchin et al. 2003). In future work, we hope to consider other consumer-resource interaction terms; for now, however, this model provides a convenient starting point. The consumer's fecundity function $f(R_i(x), C_i(x))$ is then

$$f(R_i(x), C_i(x)) = \phi R_i(x) \left[1 - \exp \left[\frac{-sC_i(x)}{(1 + \mu C_i(x))} \right] \right]. \quad (2)$$

Here ϕ is the maximum value of the consumer's reproductive rate, so resources that are attacked are converted into consumers at rate ϕ . In what follows, we eliminate the parameters a and s by rescaling resource and consumer densities according to $R_i^*(x) \equiv R_i(x)/a$ and $C_i^*(x) \equiv sC_i(x)$. We then define $\eta \equiv \rho/a$ and $\lambda \equiv \phi/a$ to be the scaled growth rates of the resource and the consumer, respectively. In the interests of brevity, in what follows we refer to η and λ simply as growth rates, and we refer to μ as the consumer-interference parameter.

Our models of the temporal dynamics are thus based on well-known consumer-resource models. What remains is to specify how consumers disperse. As we have described, we consider two models that differ in whether resources affect the probability that a consumer disperses or the distance that a consumer disperses. Because the only difference is in consumer dispersal, both models use rescaled versions of equations (1) and (2) to describe resource and consumer dynamics, respectively. The full consumer equation for the changing dispersal-fraction model is then

$$C_{t+1}(x) = \int_{-\infty}^{\infty} k(|x-y|) \gamma(R_i(y)) f(R_i(y), C_i(y)) dy + [1 - \gamma(R_i(x))] f(R_i(x), C_i(x)), \quad (3)$$

Here $f(R_i(y), C_i(y))$ is described by equation (2), and we have assumed that population growth precedes dispersal; $k(|x-y|)$ is the dispersal kernel, which describes the distribution of distances dispersed over a generation; and $\gamma(R_i(y))$ is the probability that a consumer at point y disperses such that the probability of dispersal declines exponentially from a maximum of $\hat{\gamma}$ as resource levels increase. The integral term on the right-hand side of equation (3) therefore represents dispersers arriving at x from all other locations, while the second term represents individuals produced at x that do not disperse. For this model, the rate of spread depends only on conditions at the front, so the functional form of $\gamma(R_i(y))$ has little effect on our results (see app. A). The dispersal kernel can be any probability density function, but in what follows, we generally consider only a "Laplace" or "double-exponential" kernel, in which the probability that an individual located between y and $y + dy$ disperses an absolute distance $|x-y|$ is

$$k(|x-y|) dy = \frac{b}{2} e^{-b|x-y|} dy. \quad (4)$$

Here b is the inverse of the one-sided mean dispersal distance. Note that because the dispersal kernel depends only on the absolute value of the difference between x and y , the distribution of dispersal distances is independent of a dispersing individual's location (but see Van Kirk and Lewis 1999 for a discussion of how, on a finite domain, the kernel may depend explicitly on x and y because of interactions between the disperser and the boundary). In practice, we rescale space to eliminate the parameter b .

The changing dispersal-distance model instead follows the equation

$$C_{t+1}(x) = \int_{-\infty}^{\infty} h(R_i(y), |x-y|) f(R_i(y), C_i(y)) dy. \quad (5)$$

Here $h(R_i(x), |x-y|) dy$, the probability of dispersing a distance $|x-y|$ over a generation, again follows a Laplace distribution, but now it depends not just on the distance but also on the resource density at the starting location y . Specifically, we assume that the probability that an individual located between y and $y + dy$ disperses a distance $|x-y|$ is

$$h(R_i(y), |x-y|) dy = \frac{bR_i(y)}{2} e^{-bR_i(y)|x-y|} dy. \quad (6)$$

The one-sided mean dispersal distance is thus proportional to the inverse of local resource quality, and so dispersal

distances increase as resources decline. Again, b can be eliminated by rescaling space.

In appendix A, we use the method of Kot et al. (1996) to derive an expression for the rate of invasion, or the “wave speed,” of the changing dispersal-fraction model, equations (1) and (3), by making the usual assumption that the population dynamics behind the front have no effect on the wave speed. This expression turns out to accurately predict the wave speed in numerical integrations; for the changing dispersal-distance model, equations (1) and (5), however, the dynamics behind the front do affect the wave speed, and so a similar calculation is not possible. Moreover, because the changing dispersal-distance model has a spatially inhomogeneous kernel, the only method for numerically analyzing that model of which we are aware uses the trapezoidal rule for calculating the integral in equation (5). We therefore used this method to numerically integrate both models. In all cases, we began these integrations by setting resource levels to their consumer-free equilibrium everywhere in space and then setting consumer density near the origin to a low level. Also, in calculating the rate of spread of the consumer, we must pick a point \hat{x} that defines the front of the wave. Because for both models the front declines gradually with increasing distance, there is no natural choice of \hat{x} , and so we chose \hat{x} such that $C_i(\hat{x}) = 0.01$. For the parameter values that we used, this choice avoids densities that are so low as to be difficult to measure, but it is still low enough to qualify as being at the front of the wave. Moreover, the shape of the front for both models is similar across parameter values, and so our results are independent of the value of \hat{x} as long as the consumer density at \hat{x} is not too large.

Results

As in most invasion models, the changing dispersal-fraction model shows traveling waves with constant shape and velocity (fig. 1). If the resource or consumer growth rates η and λ are relatively low and the consumer-interference term μ is relatively high, then consumer density forms an advancing front that trails off to high levels behind the front (fig. 1A, 1B). In contrast, if η or λ is relatively high and μ is relatively low, then resources decline rapidly behind the wave, and consumer density forms an advancing peak (fig. 1C). Moreover, in this latter case, trains of waves appear behind the initial peak such that the initial peak of invasion is repeated behind the front. In either case, speeds calculated by numerical integration of equations (1) and (3) are very close to the wave speed calculated by assuming that population dynamics behind the front do not matter (fig. 2; see app. A for the calculation). Figure 2A shows that because the invasion fails

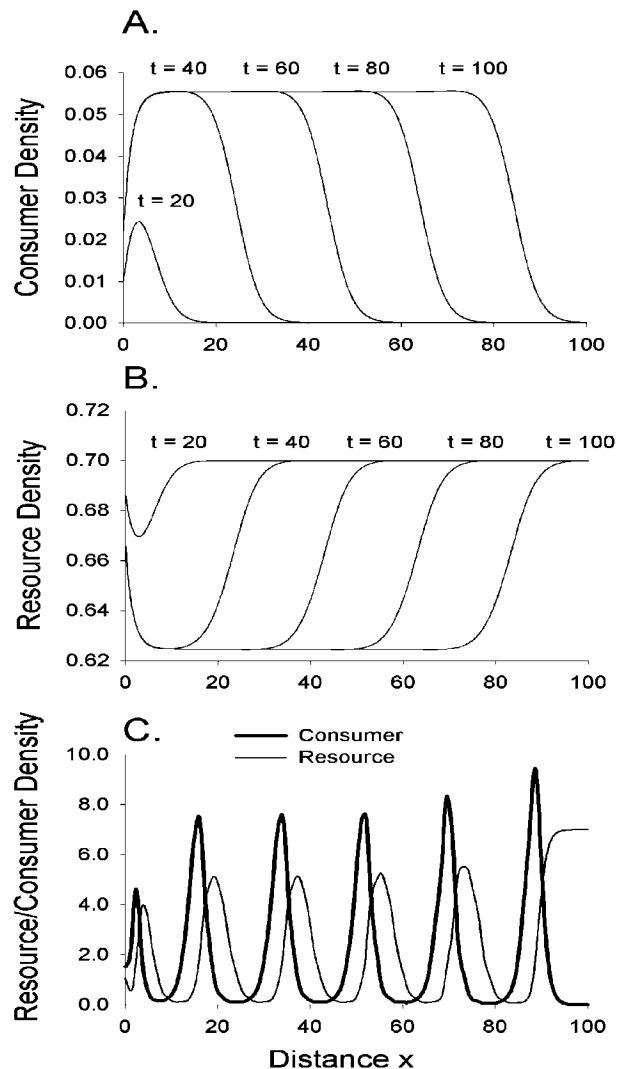


Figure 1: Model results for the changing dispersal-fraction model, equations (1) and (3). A, B, Consumer and resource densities versus distance from the point of introduction x . $t = 20$, and so forth, indicates the number of generations that have elapsed. Note that, for clarity, B has a different scale than A. Parameters for A and B are as follows: resource growth rate $\eta = 1.7$, consumer-interference parameter $\mu = 4$, maximum probability of dispersing $\hat{\gamma} = 0.5$, consumer reproductive rate $\lambda = 2$. C, Snapshot of consumer and resource densities for a set of parameter values that gives trains of waves. Here $\eta = 8$, $\mu = 0.15$, $\hat{\gamma} = 0.5$, $\lambda = 2$, and $t = 120$.

altogether when $\lambda < 1$, the wave speed is rather sensitive to the consumer reproductive rate λ when λ is near 1 and thereafter increases as roughly the natural log of λ . A similar result holds for the effect of the resource growth rate η ; indeed, although in the interests of brevity we do not show it here, figure 2A would look the same if we instead plotted wave speed against $\eta - 1$ (app. A). The fraction

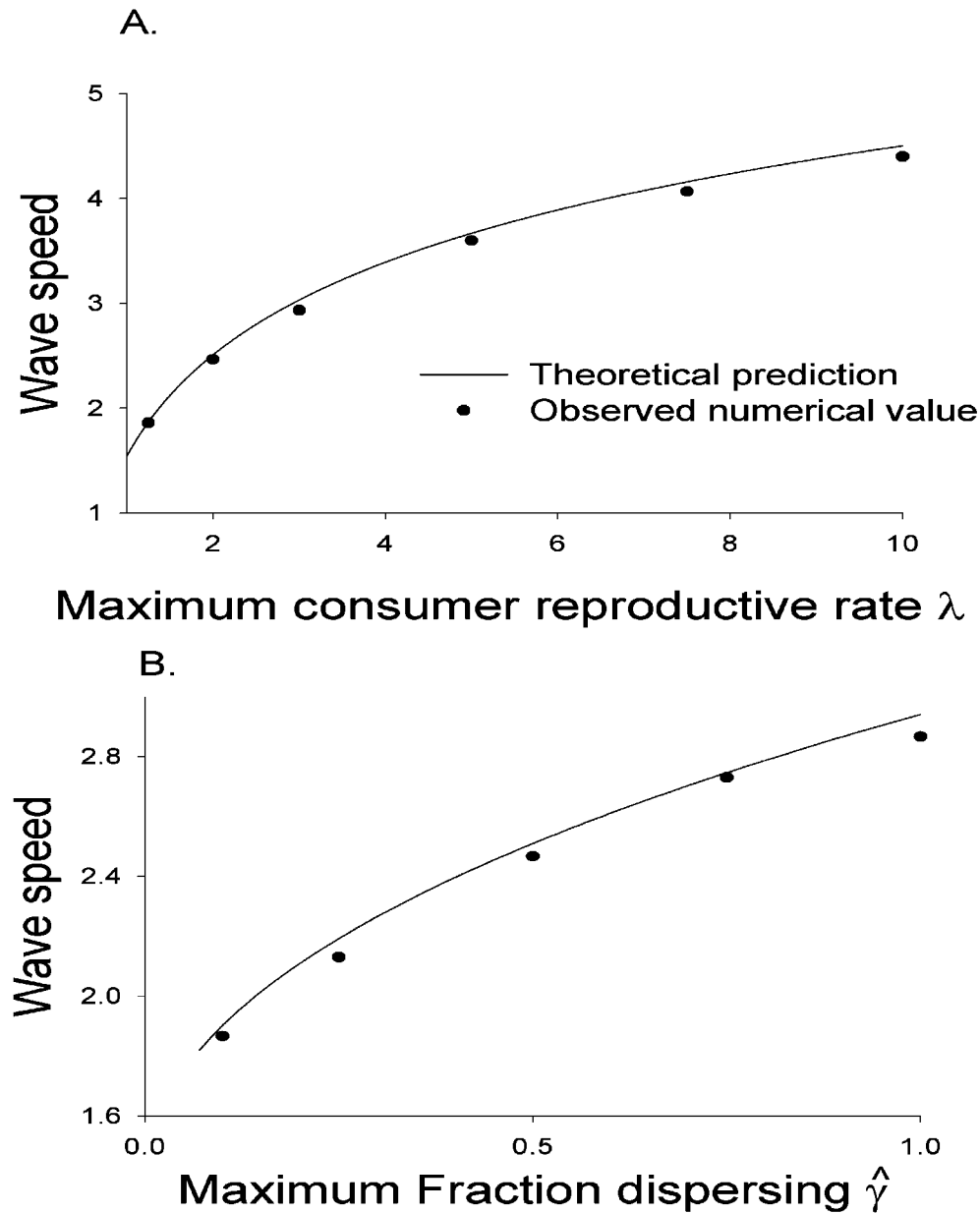


Figure 2: Wave speed calculated by numerical integration compared with the theoretical wave speed calculated in appendix A for different values of λ (A) and $\hat{\gamma}$ (B). Remaining parameters are as in figure 1A and 1B. Wave speed is expressed as distance moved per generation. Because distance is scaled so as to be dimensionless, no units are given on the vertical axis.

dispersing at the front $\hat{\gamma}$ has a more modest effect on the wave speed (fig. 2B). In general, these results are similar to those of Kot et al. (1996), with the difference that in our model, the wave speed is affected by the probability of dispersing when consumer density is low, $\hat{\gamma}$. In fact, if we set $\hat{\gamma} \equiv 1$ and if we define the effective consumer reproductive rate to be $\lambda \times (\eta - 1)$, the wave speed in our model is identical to the wave speed in the Kot et al. (1996)

model; in turn, this means that with a normal dispersal kernel, our model would show the same wave speed as the classic Fisher model (Fisher 1937). Significantly, the consumer-interference term μ never has any effect on the rate of spread of the consumer because it affects only the dynamics behind the front.

The changing dispersal-distance model also shows traveling waves, but the behavior of these waves is dramatically

different. The basic difference is that, as figure 3A shows, the consumer-interference parameter μ strongly affects the wave speed. Moreover, if either the resource growth rate η or the consumer reproductive rate λ is sufficiently high relative to μ , then the wave speed fluctuates, as shown in figure 3. Because μ becomes important only after the consumer has become established, it therefore appears to be the case that, in contrast to the changing dispersal-fraction model, for this model, the population dynamics behind the front affect the rate of spread of the invader. Moreover, in general, the wave speeds for the changing dispersal-distance model are much higher than for the changing dispersal-fraction model, even when the nondispersal parameters are the same. To see this, note first that η is the same in figures 2A and 3A. Figure 2A then shows that the wave speed for the changing dispersal-fraction model is almost 3 when $\lambda = 3$; in contrast, even though $\lambda = 3$ in

figure 3A, the average wave speed instead ranges from approximately 25 to approximately 80, depending on the value of μ . Allowing resource levels to affect the distance dispersed thus leads to much higher wave speeds and allows the population dynamics behind the front to affect the wave speed.

As we discuss further in appendix B, the fluctuations in the rate of spread do not appear to be artifacts of our numerical approximation scheme but instead are apparently a basic feature of the model. Understanding why the wave speed fluctuates, however, is difficult. One possible explanation is that a consumer-resource cycle may be occurring behind the wave front. Indeed, in all cases in which the wave speed fluctuates, trains of waves appear behind the front, similar to the wave trains in figure 1C. We therefore suspected that periods of high consumer density behind the wave might cause the wave to accelerate, while

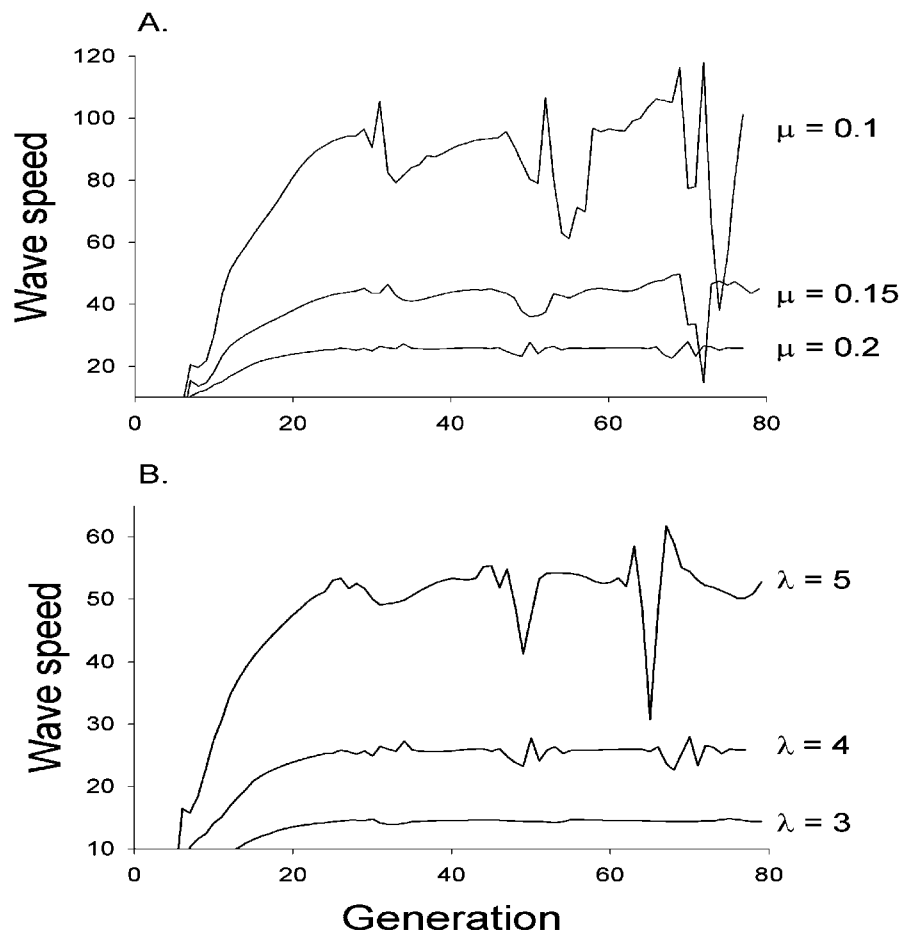


Figure 3: Wave speeds versus time for the changing dispersal-distance model, equations (1) and (5), for different values of the consumer-interference parameter μ and the consumer growth rate λ . In all cases, the resource growth rate $\eta = 3$. *A*, In all cases, $\lambda = 4$. *B*, In all cases, $\mu = 0.2$. Wave speed is expressed as dimensionless distance moved per generation.

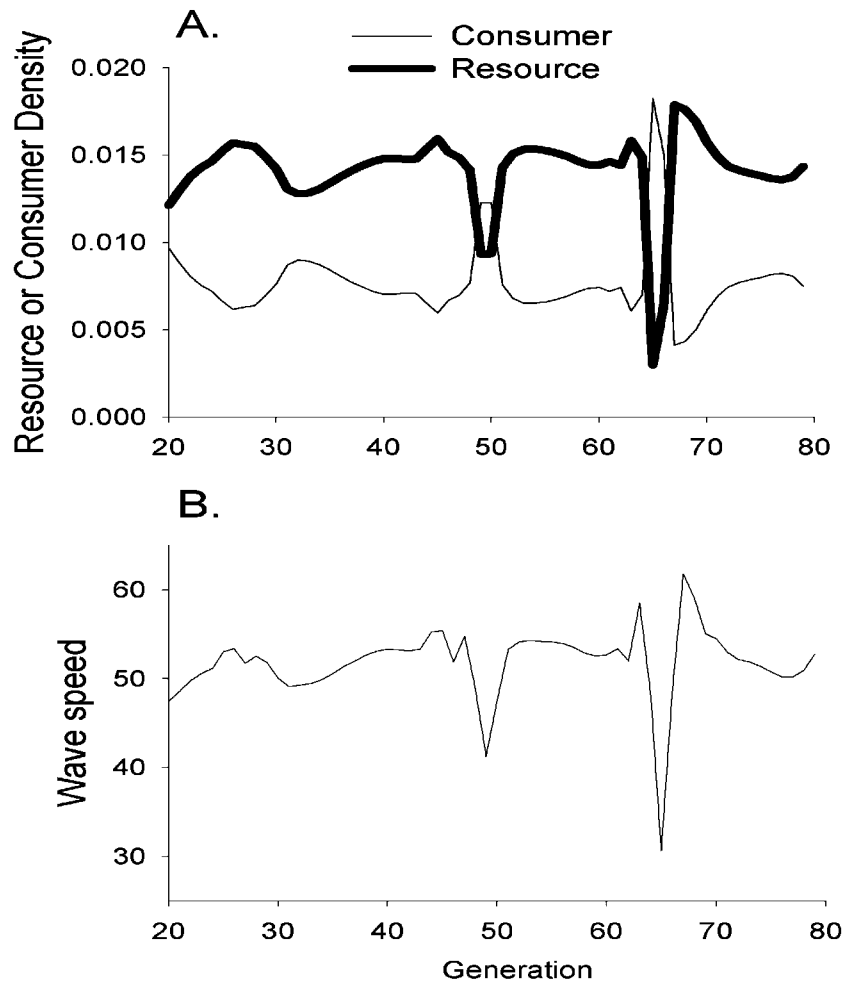


Figure 4: Comparison of wave speed to the consumer-resource population dynamics behind the wave. *A*, Consumer and resource densities averaged over 100 distance units behind the wave front. Parameters are the same for *A* and *B*: resource growth rate $\eta = 3$, consumer growth rate $\lambda = 5$, species interaction parameter $\mu = 0.2$. *B*, Wave speed versus time for the changing dispersal-distance model, equations (1) and (5). Wave speed is expressed as dimensionless distance moved per generation.

the opposite conditions would cause the wave to decelerate. To look for such cycles, we averaged resource and consumer densities behind the wave according to

$$\hat{R}_t \equiv \frac{1}{L} \int_{\hat{x}-L}^{\hat{x}} R_t(x) dx, \quad (7)$$

$$\hat{C}_t \equiv \frac{1}{L} \int_{\hat{x}-L}^{\hat{x}} C_t(x) dx, \quad (8)$$

where \hat{R}_t and \hat{C}_t are the average densities of resources and consumers, respectively, over a distance L behind the front

and \hat{x} is again defined as the leading edge of the front. In general, we expect that the influence of the population dynamics behind the front will decline with increasing distance behind the front, but there is no obvious choice of L , and so we arbitrarily used $L = 100$.

Figure 4A shows the fluctuations in \hat{R}_t and \hat{C}_t , suggesting that there is in fact some kind of consumer-resource-type oscillation behind the wave front. Indeed, in this particular case, it appears that the amplitude of the fluctuations is increasing. Moreover, the fluctuations in the resource density seem to be closely synchronized with the fluctuations in the wave speed (fig. 4); that is, peaks and troughs in resource density occur at nearly the same time as peaks and troughs in the rate of spread. Because peaks in resource density correspond to troughs in consumer density, how-

ever, the most likely explanation is that the rate of spread is driven by the number of consumers, with a slight delay. When the number of consumers rises to a peak, shortly afterward the rate of spread accelerates because more consumers are available to disperse, and when the number of consumers falls to a trough, shortly afterward the rate of spread decelerates because fewer consumers are available to disperse.

To further explore the importance of consumer-resource cycles for velocity oscillations, we compared the dynamics of this model with the dynamics of the analogous nonspatial model. Simulations showed that the parameter values that give oscillatory velocities in figure 3 give limit cycles in the nonspatial model and that parameter values that give constant velocities in the spatial model give a stable equilibrium in the nonspatial model. As an example of this behavior, figure 5 shows output for two sets of parameter values on either side of the limit-cycle boundary for the nonspatial model. In figure 5A, the consumer growth rate $\lambda = 3.1$, which is below the critical value of $\lambda \approx 3.2$, and the oscillations appear to damp out. In figure 5B, $\lambda = 3.8$, which is above the critical value, and the amplitude of the oscillations appears to be increasing. These results are consistent with the hypothesis that the boundary between stable cycles and a point equilibrium for the nonspatial model is also the boundary between a constant and a fluctuating wave speed for the spatial model. As discussed further in appendix B, the simulations of the spatial model are so time intensive that we have not yet found a case in which the amplitude of the velocity oscillations has clearly stabilized. If the cycles in the spatial model are in fact unstable, then the amplitude of velocity fluctuations will increase without bound; nevertheless, even if such instabilities eventually arise, clearly the cycles persist long enough to be biologically important.

Discussion

Our models suggest that resource-dependent dispersal can have significant consequences for invasions but that the effect depends on the details of how resources affect dispersal. If resources affect only the probability of dispersal, then spread rates are essentially no different than if dispersal is completely unaffected by resources (fig. 2). If resources instead affect the distance dispersed, however, then the spread rate is much higher, and complex population dynamics behind the wave front can lead to fluctuations in the rate of spread (figs. 3–5). This behavior is strikingly different from that of other models of spatial spread. In particular, two basic results of most invasion models are that spread rates will be unaffected by the dynamics behind the front and that long-term wave speeds are constant (Fisher 1937). Here we have shown that in

fact neither conclusion is general. Moreover, although some other models show modest effects of population dynamics behind the front on the wave speed (Lewis and Kareiva 1993; Shigesada and Kawasaki 1997; Wilson and Richards 2000), in no case are there sustained fluctuations in wave speeds. The fluctuating wave speed and the strong effects of population dynamics behind the front in our model thus appear to be novel results.

These results are of more than mere mathematical interest, however, because our changing dispersal-distance model is appropriate for a large class of organisms. To begin with, organisms with discrete generations are common in temperate zones, especially among insects, an important class of invading species (Andow et al. 1990). We suspect that the results of our models also hold for organisms with overlapping generations but discrete breeding seasons, another large class of invading species, because models with overlapping generations but discrete breeding often have dynamics that are as complicated as models with discrete generations (Gurney and Nisbet 1998). More critically, our assumption that resources affect dispersal distances holds for many organisms. As we described in the introduction to this article, many species show area-restricted search (Segel 1977; Kareiva and Odell 1987; Morris and Kareiva 1991; Keasar et al. 1996; Turchin 1998; Fryxell et al. 2004), and in such cases dispersal distances are likely to be high over both short and long time scales when resources are low. In addition, there are many examples in the literature of direct evidence for effects of resources on dispersal distances (Reznik 1991; Kuussaari et al. 1996; Goodwin and Fahrig 2002; Pasinelli and Walters 2002; Byholm et al. 2003; Cronin 2003). Indeed, recent work in G. Dwyer's lab has shown that resources affect the distance that treehoppers *Publilia concava* (Homoptera: Membracidae) move within patches of narrow-leaved goldenrods *Solidago altissima* (S. M. Harrell Yee and G. Dwyer, unpublished manuscript). Nevertheless, it is inherently more difficult to quantify the distance dispersed than to quantify the probability of dispersing (Harrison and Karban 1986; Hunter and Lechowicz 1992; Nealis and Lomic 1994; Herzog 1995; Rhainds et al. 2002; Rhainds and Shipp 2003). Indeed, behaviors such as area-restricted search are usually studied over time periods substantially shorter than a generation. Nonetheless, because whole-generation dispersal distances are the cumulative result of shorter-term movement behaviors, it is highly likely that short-term movements in response to resources translate into resource-dependent dispersal distances over a generation. Given the logistic difficulties of measuring resource-dependent dispersal distances, we suspect that this type of dispersal is even more common than the literature indicates.

The second reason why the results of the changing

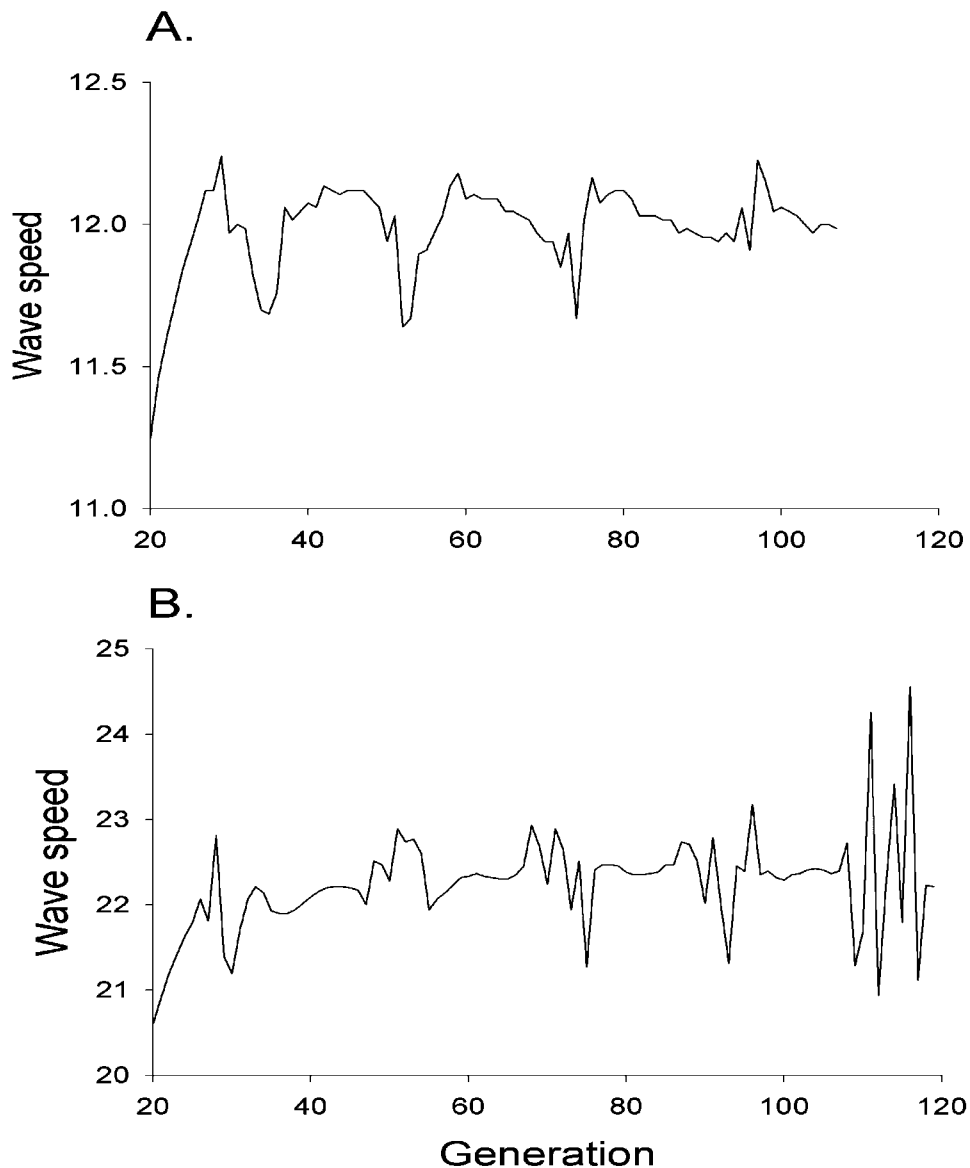


Figure 5: Wave speeds for the changing dispersal-distance model, equations (1) and (5). In both *A* and *B*, the resource growth rate $\eta = 3$, and the species interaction parameter $\mu = 0.2$. *A*, Here the consumer growth rate $\lambda = 3.1$. This value is on the stable side of the limit-cycle boundary for the nonspatial version of the model. Note that the oscillations appear to damp out with time. *B*, Here the consumer growth rate $\lambda = 3.8$. This value is on the cyclic side of the limit-cycle boundary for the nonspatial version of the model. Note that the amplitude of the oscillations appears to increase with time. Wave speed is expressed as dimensionless distance moved per generation.

dispersal-distance model are important is that the model shows that the effects of resources on distances dispersed can have striking biological consequences. The first of these consequences is that invasions can be a multispecies phenomenon. That is, the effect on the wave speed of the consumer-interference parameter μ , which essentially modulates the interaction between the consumer and the resource, shows that a species invasion can depend on

species interactions. In contrast, the lack of any such effects in classical models has led to the widespread view that invasions are fundamentally a single-species phenomenon (Murray 1991). Moreover, this result has direct practical implications for the management of invading species. Because the invasion speed can be affected by conditions behind the front, management efforts aimed at reducing the density of an invader behind the front not only may

mitigate its local impact but also may have the added benefit of decreasing the rate at which it spreads. This is an important point because efforts to slow the spread of invading species generally focus only on dynamics at the front (Sharov et al. 2002). In addition, if resources affect dispersal distances, then efforts to predict invasion speeds that are based only on data collected at the wave front may not give reliable results. In such cases, accurate prediction of invasion speeds will also require that we quantify how resource levels change behind the wave. Although estimating the parameters of resource-dependent models thus requires more data, our work suggests that the increase in accuracy of the resulting predictions may be substantial. Also, one possible test of our model would be to reduce the density of an invading consumer by introducing a predator or pathogen behind the wave front as a means of biological control. If such an introduction leads to a reduction in the rate at which the consumer is spreading, then the reduction in spread rate would support the model. To our knowledge, such a test has not yet been carried out. Finally, the occurrence of fluctuating velocities of spread in the changing dispersal-distance model may provide an explanation for at least some cases of changing wave speeds (Andow et al. 1990; Leibhold et al. 1992; Shigesada and Kawasaki 1997). Again, however, a thorough test of this prediction will likely require additional data because to our knowledge, time series of invasion rates that are long enough to show sustained fluctuations (figs. 3, 5) do not yet exist.

The difference in the outcomes of our two models shows that modest differences in behavior can have significant population-level consequences. This result emphasizes the important role that mathematical models can play in guiding our understanding of spatial phenomena. In particular, as we described in the introduction to this article, it seems intuitively reasonable that resource-dependent dispersal will affect the rate of spread of invasions. Comparison of our previous work (Morris and Dwyer 1997) with the work that we present here, however, shows that the effects of resource-dependent dispersal are negligible when reproduction and movement occur continuously and thus that time delays play an important role in modulating the effects of dispersal. More generally, our work suggests that an important future research direction for models of invasions is the further investigation of discrete-generation models in which densities affect dispersal distances. Indeed, the difficulty of numerically integrating the changing dispersal-distance model argues for the development of more sophisticated numerical methods (app. B). That said, it is worth noting that our basic results are the same if we instead use a model based on discrete-time versions of logistic growth and Lotka-Volterra predator-prey functions (G. Dwyer and W. F. Morris, unpublished manuscript).

Also, because we are interested in general theoretical results, we have used simple dispersal kernels. For practical applications, it may be useful to consider a model in which area-restricted search over the short term, which is typically described by continuous-time partial differential equations (Segel 1977; Kareiva and Odell 1987), is translated into dispersal over the course of a generation, as in our integrodifference equation models. A useful feature of such a hybrid model is that it would be easier to parameterize with existing data. That is, most data showing effects of resources on movement distances do not track organisms for entire generations because as we have described, such tracking is often logistically impractical. A hybrid model would therefore make it easier to relate complex behaviors to long-term spread rates.

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APPENDIX A

Calculating the Minimum Wave Speed for the Changing Dispersal-Fraction Model

Here we follow Kot et al. (1996, app. A) in calculating the invasion speed for the model, equations (1) and (3), under the assumption that the dispersal kernel $k(z)$ has a moment-generating function. First, given our assumption that $\gamma(R_t(x)) = \gamma_0 \exp(-R_t(x))$, and given that the equilibrium density of the resource ahead of the wave is $\eta - 1$, we define $\hat{\gamma} = \gamma_0 \exp[-(\eta - 1)]$ to be the fraction dispersing far ahead of the wave. Second, if the invasion speed is determined only by the behavior of the population near the front (where resources are abundant and consumers are scarce), we can linearize equation (3) near the consumer-free equilibrium $(R_t(x), C_t(x)) = (\eta - 1, 0)$ to yield

$$C_{t+1}(x) = \int_{-\infty}^{\infty} k(x-y)\hat{\gamma}(\eta-1)\lambda C_t(y)dy + (1-\hat{\gamma})(\eta-1)\lambda C_t(x). \quad (\text{A1})$$

If the invasion proceeds as a wave with fixed shape and constant speed c , then $C_{t+1}(x) = C_t(x-c)$. Given this fact,

and with the conjecture that the wave front is exponentially bounded so that $C_i(x) \approx e^{-sx}$, equation (1) becomes

$$e^{sc} = \hat{\gamma}(\eta - 1)\lambda \int_{-\infty}^{\infty} k(x - y)e^{s(x-y)} dy + (1 - \hat{\gamma})(\eta - 1)\lambda. \quad (\text{A2})$$

Making the change of variable $u \equiv x - y$ and recognizing that $M(s) \equiv \int_{-\infty}^{\infty} e^{su}k(u)du$ is the moment-generating function of $k(z)$, we arrive at

$$e^{sc} = \hat{\gamma}(\eta - 1)\lambda M(s) + (1 - \hat{\gamma})(\eta - 1)\lambda. \quad (\text{A3})$$

Taking the derivatives of both sides of equation (3) with respect to s yields $ce^{sc} = \hat{\gamma}(\eta - 1)\lambda M'(s)$, and combining this expression with equation (3) gives the invasion speed as a function of s :

$$c = \frac{\hat{\gamma}M'(s)}{\hat{\gamma}M(s) + 1 - \hat{\gamma}}. \quad (\text{A4})$$

Note that for $\hat{\gamma} \equiv 1$ and invader growth rate equal to $\lambda(\eta - 1)$, equations (3) and (4) are equivalent to equations (9a) and (9b) of Kot et al. (1996).

So far, we have made no assumptions about the shape of the kernel. To proceed further, we specify that $k(z)dz = (b/2)\exp(-b|z|)dz$. Because we can eliminate b by an appropriate scaling of the spatial dimension, however, our expressions for the moment generation function and its derivative are $M(x) = 1/(1 - s^2)$ and $M'(s) = 2s/(1 - s^2)$. Equation (4) therefore becomes

$$c = \frac{2s}{(1 - s^2) + [(1/\hat{\gamma}) - 1](1 - s^2)^2}. \quad (\text{A5})$$

Given values of $\hat{\gamma}$, η , and λ , we can compute s by substituting equation (5) in place of c in equation (3) and using a root-finding algorithm to obtain s . Substituting the resulting value into equation (5) yields the invasion speed.

APPENDIX B

Numerical Instabilities in the Changing Dispersal-Distance Model

A key feature of the fluctuations in the wave speed is that they are somewhat irregular in appearance even though the cycles in the nonspatial version of the model are, in contrast, quite regular. It was important to consider whether this irregularity was due merely to numerical er-

ror, because such errors might also explain the occurrence of wave speed fluctuations themselves. Ultimately, it is not possible to make such a determination without a mathematical proof, but such proofs are beyond the scope of our work, and so we tested our numerical routine in the following way. Our numerical integrations of the model require that we approximate the spatial domain of the models using a discrete grid. As the number of grid points increases for a given spatial domain, the resolution of the grid increases, and thus the error is reduced. Reassuringly, for spatial domains large enough to permit 80 generations of spread, grid sizes of 2×10^5 or 2.5×10^5 points gave essentially identical results to grids of 1×10^5 points. Nevertheless, simulations with that many grid points often took more than 10 days for a single run using one node of a Beowulf computer cluster. It was therefore not practical to carry out our integrations for more than 120 generations, and so we do not know whether the limit cycles in our model are stable, or “super-critical,” as opposed to unstable, or “subcritical” (Kuznetsov 1995). To our knowledge, however, most data sets for invading species are much shorter than our model runs, suggesting that longer runs would be of limited biological interest.

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