

Interacting Effects of Disturbance and Dispersal on Individual Selection and Population Stability

This paper reviews theoretical predictions regarding the interacting effects of disturbance and dispersal on individual selection and population stability. Following Rykiel,¹ I define disturbance as any external force that causes a detectable perturbation to an ecological system. Given this definition, it becomes clear that the ways in which population biologists use the terms "temporal variability," "spatio-temporal variability" or simply "variability" are often synonymous with usage of the term "disturbance" by community and ecosystem ecologists. In addition to summarizing existing theory concerning the interplay of disturbance and dispersal, I present new analyses that show how dispersal can either enhance or reduce population stability, depending on the level of disturbance and the dispersal rate. Finally, I review the empirical data that address disturbance and dispersal theory and suggest profitable areas for future research.

INTRODUCTION

One of the most obvious features of ecological systems is that they are frequently subject to environmental variability or "disturbances." Events such as hurricanes, fires, and earthquakes often come to mind when one thinks of ecological disturbance. However, for organisms that respond to the environment at small scales, the death of a single tree, the digging of a gopher mound, or the overturning of a rock in a stream may also cause considerable environmental variability. Since disturbances are common at all scales, it is not surprising that ecologists have built a good deal of both verbal theory and mathematical theory to deal with this phe-

Comments Theoretical Biology
1990, Vol. 1, No. 5, pp. 275-297
Reprints available directly from the publisher
Photocopying permitted by license only

© 1990 Gordon and Breach,
Science Publishers S.A.
Printed in Great Britain

nomenon. However, because the kinds of disturbances are highly variable, it is also not surprising that the literature is somewhat disjointed; findings on issues related to disturbance are not integrated into a well-defined body of knowledge.

One area in which there is a notable lack of synthesis is the study of how dispersal of organisms affects the impact of disturbance on individual fitness and population stability. Several models have included both disturbance and dispersal, but the results have not been integrated into one body of theory. In this paper I redress this void by reviewing themes and questions from the theoretical population biology literature on disturbance and dispersal.

Definitions

Population Stability. When ecologists say that a population is stable they can mean several different things. They may mean that if the population size is changed slightly, it will return to an equilibrium point. More commonly, they may mean that the amplitude of population fluctuations is usually low relative to the mean population size, or that there is a low probability (per unit of time) of population extinction. These last two definitions of stability can be combined since widely fluctuating populations are more prone to extinctions than those having smaller fluctuations (relative to the mean).

Individual Selection. Individual selection refers here to selection for specific phenotypic characteristics; in this review I focus on characteristics of dispersal behaviour. Theoreticians have used two approaches to examine the selective advantage of dispersal characteristics: (i) an evolutionarily stable strategy analysis in which one identifies the strategy (*i.e.*, phenotypic characteristic) that gives the individual higher fitness than any possible alternative strategy, and (ii) an optimization analysis in which one determines the strategy that results in the highest population growth rate.

Dispersal. Dispersal refers to a change in location of organisms, accompanied by reproduction. Reproduction can occur after the move to the new area, or the organisms may reproduce in the original area, and their offspring disperse to a new one. Reproduction must be included so that movements such as foraging that

bring the organism back to its starting point are not treated as dispersal events. In this review I define "dispersal rate" as the fraction of organisms that disperse from a local population.

Disturbance. Arriving at a precise definition of ecological disturbance is problematic. Grime² defines disturbance as "the mechanisms which limit biomass by causing its partial or total destruction." This is similar to the traditional concept of a disturbance as "an event that is massively destructive and rare."¹ However, this definition no longer encompasses the range of ideas included in the modern concept of ecological disturbance.^{1,3,4} White and Pickett⁵ define disturbance as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment." This definition is broader than Grime's since it includes positive or negative changes. However, it does not specify whether disturbance is a cause or an effect, or whether it is internal or external to the system of interest. This imprecision is at the root of the problem described by DeAngelis *et al.*⁶ They point out that a treefall in a forest may be caused by a combination of wind (an external force) and tree ageing (an internal process), and they ask whether this disturbance (the gap in the forest canopy) is exogenous or endogenous.

The definition proposed by Rykiel¹ seems to be the best combination of generality and precision. He defines disturbance as "A cause; a physical force, agent, or process, either biotic or abiotic, causing a perturbation in an ecological component or system; relative to a specific reference state and system." The system under study must be precisely defined, the undisturbed "reference state" of the system must be defined, and the term disturbance refers only to a cause ("force, agent or process"), while "perturbation" refers to the effect of the disturbance. The disturbance must be external to the system.

It should be noted (as does Rykiel) that the distinction between disturbance and perturbation is often not made in the literature; disturbance often is used to designate both the cause and the effect. This does not normally cause difficulties, so I will continue this tradition here unless an ambiguity arises. If we use Rykiel's definition, the problem described by DeAngelis *et al.* (above) is cleared up; the wind is a disturbance, the gap is a perturbation (not a

disturbance), and the tree ageing is internal to the system and therefore not a disturbance.

Note that a force may or may not be a disturbance depending on how one defines the system. For example, if the system is defined as a particular population, then predation on that population is a disturbance if it causes a perturbation. However, if one defines the system as a whole community including predator and prey, the predation is internal to the system and therefore not a disturbance. A similar situation may occur with competition. For example, *Pieris virginienis*, a specialist herbivore, suffers population crashes during occasional outbreaks of gypsy moth.⁷ The gypsy moth is not normally a competitor for the food plant of *P. virginienis*, but during outbreak conditions it consumes plants not normally in its diet, and therefore becomes an important competitor for *P. virginienis*. If the system here is defined as the population of *P. virginienis*, a gypsy moth outbreak is a disturbance.

An Issue of Semantics

Since I am using Rykiel's¹ definition of disturbance in this paper, externally caused temporal variability is synonymous with disturbance. However, it should be noted that in the theoretical literature of population biology the word "disturbance" is not normally used; usually "temporal variability," "spatio-temporal variability," or simply "variability" are used instead. In fact, "disturbance" seems to be used almost exclusively in the community ecology and ecosystem literature, usually in combination with ideas about competition and succession or nutrient and energy cycling (see, for example, most chapters in Mooney and Godron⁸ and Pickett and White⁹). Since in this paper I am dealing with single-species studies, most of the papers I will be referring to do not actually use the word "disturbance." However, as currently used in the literature, disturbance in community and ecosystem studies is the same concept as variability in population studies. The importance of this point is seen in the statement of Pickett and White⁹ that there are currently two hypotheses concerning disturbance in the literature. Both of the hypotheses to which they refer deal with communities. The fact that there are many population-level hypotheses has escaped their attention because of the semantic problem.

In the theoretical literature of population dynamics and individual selection, disturbance is included in models in several ways. In analytical models, one often allows the parameter(s) of standard deterministic models to vary in some random fashion. Turelli¹⁰ refers to this as "environmental stochasticity," while Chesson¹¹ refers to this as "pure temporal variation" or "spatiotemporal variation." A simple example of this kind of modeling approach is illustrated by May,¹² in which he studied the logistic equation

$$dN(t)/dt = N(t)[k - N(t)] \text{ with } k = k_0 + \tau(t), \quad (1)$$

where N is the population size, t is time, and k is the carrying capacity of the environment. k fluctuates randomly about the mean value k_0 according to a Gaussian "white noise" process $\tau(t)$ which has mean zero and variance σ^2 .

Two other approaches for applying variability to a model are used in simulation modeling. First, one may apply a noise term to the population equation as a whole; each time step in the simulation model there is a random fluctuation (positive or negative) applied to the calculated population size. For example

$$N_{t+1} = rN_t(k - N_t) + \delta, \quad (2)$$

where N_{t+1} is the population size at time $t + 1$, r is the population growth rate, k is again the carrying capacity and δ is a random variable, often a Gaussian noise term as above. The second approach is to simply eliminate some portion of the population when a disturbance occurs in the simulation. This may involve random elimination of local populations, or periodic or aperiodic reductions in total population. This method more closely approximates the traditional definition of disturbance as a large destruction of biomass.

The Main Issues in Disturbance and Dispersal Theory

The two main questions that disturbance and dispersal theory deals with are (i) what dispersal level will natural selection favor under different disturbance regimes? and (ii) what is the influence of dispersal on population stability in different disturbance regimes? These two issues, evolution of optimal dispersal rate and popu-

lation stability, are not independent. As stated by Sousa,¹³ "For a fugitive species to persist, disturbances must generate colonisable space within the dispersal range of extant populations and within the period of time it takes for those populations to go extinct. Dispersal distance and the time to local extinction are functions of the life history of the particular species as well as local population density."

RESULTS AND HYPOTHESES

Individual Selection

Life History Strategies: Verbal Theory. The first major statement of the interacting effects of disturbance and dispersal was in the *r-K* life history continuum of MacArthur and Wilson.¹⁴ One component of this theory is the prediction that species living in environments that are frequently disturbed should have high rates of dispersal. They suggest that high dispersal rates evolve to allow organisms to escape from unfavorable areas, and colonise favorable ones.

A similar idea is the "risk-spreading" hypothesis of den Boer.¹⁵ He suggested that, if disturbance can cause the extinction of local populations, and if disturbances occur at different times in different places, an organism whose offspring disperse widely will stand a good chance of distributing some of them to patches of habitat where a disturbance does not occur. This will ensure that at least some offspring survive. In an extension of the *r-K* argument Holm¹⁶ suggests that three different dispersal strategies may occur depending on the type of disturbance typically experienced: (i) the "opportunistic" highly dispersive strategy is expected if disturbance is moderately common, but the time and place of disturbance events is unpredictable, (ii) the rhythmic or seasonal dispersal strategy is expected if disturbance is predictable in time (e.g., it is seasonal), and (iii) the low or no dispersal strategy is expected if disturbance is so frequent that the habitat is predictably unfavorable, and there is no longer any advantage to dispersal (an idea also suggested by Levin *et al.*¹⁷).

Evolutionarily Stable Dispersal Strategies. A rigorous treatment of

the interplay between dispersal strategies and disturbance involves the analysis of "Evolutionarily Stable Strategy" (ESS—Maynard Smith¹⁸). The evolutionarily stable strategy is defined as the strategy that results in the highest individual fitness under specified conditions. Figure 1A-C illustrates the results of such analyses,^{17,19,20} in which the optimal dispersal rate is determined for different levels of environmental variability (*i.e.*, disturbance). The general result is that the optimal dispersal rate increases with

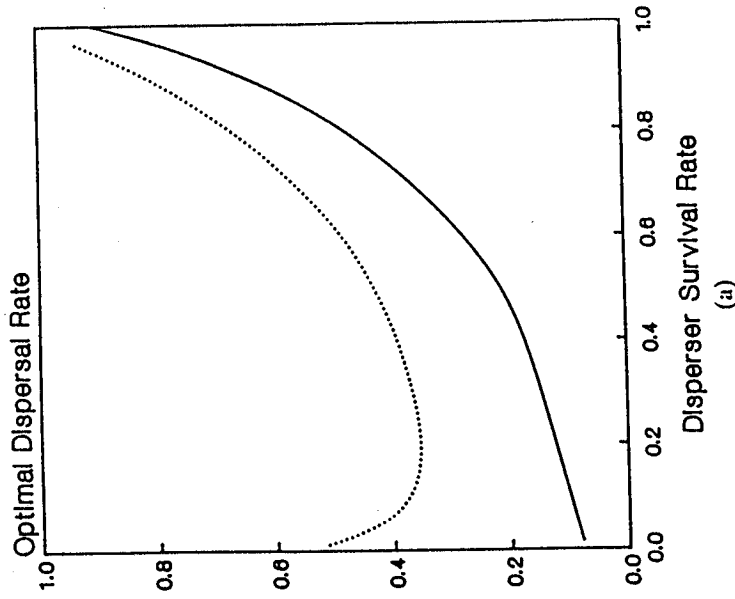
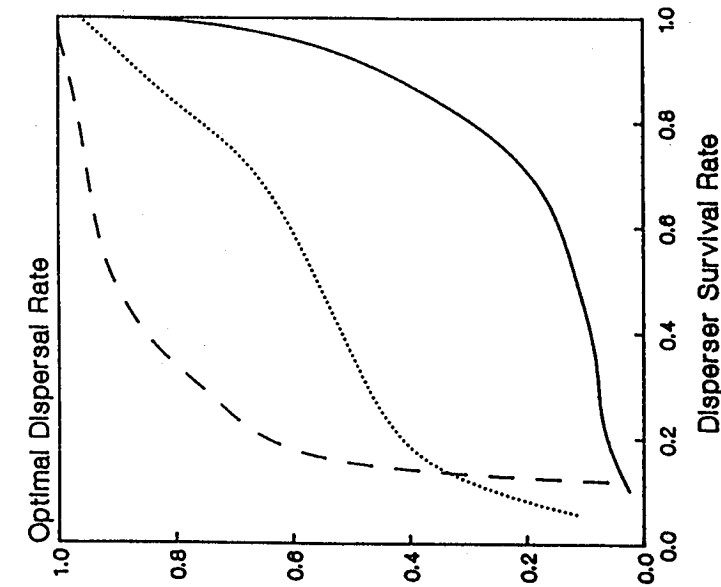


FIGURE 1 Optimal dispersal rate as a function of disperser survival rate for different levels of disturbance, taken from three different theoretical studies. A. Redrawn from Comins *et al.*,¹⁹ Figures 2 and 4. Disturbance level is probability of local extinctions (x) per unit time. Solid line: $x = 0$, dotted line: $x = 0.1$. B. Redrawn from Levin *et al.*,¹⁷ Figures 5, 6, and 7. Disturbance level is the maximum of p that the maximum local population size is 1 (vs. an alternative maximum of 100) (per time unit). Solid line: $p = 0.1$, dotted line: $p = 0.5$, dashed line: $p = 0.9$. C. Redrawn from Klinkhamer *et al.*,²⁰ Figure 7. Disturbance level is the squared coefficient of variation (c.v.²) of the number of progeny per seedling among local populations over time. Solid line: c.v.² = 1, dotted line: c.v.² = 2.

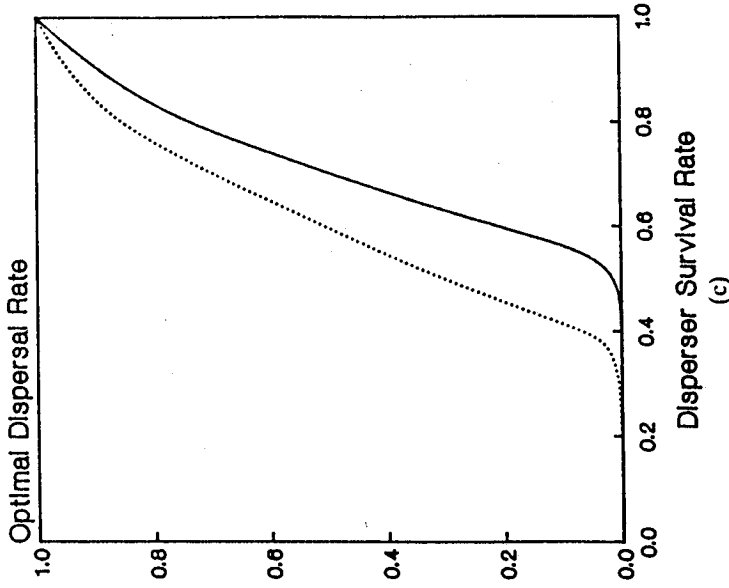


(b)

FIGURE 1 (continued)

increasing disturbance probability. This result supports the idea that dispersal reduces the chance of an individual leaving no or few offspring.

The differences in the shapes of the curves from these three studies demonstrate that the particular method of including disturbance in a model may affect the qualitative predictions. Comins *et al.*¹⁹ model predicts an increase in optimal dispersal rate if dispersers have low survival, when the disturbance level is high (Figure 1A, dotted line). In this model disturbance is modeled explicitly as the probability of local population extinction. It appears that there is a minimal rate of re-establishment of extinct local populations required in order for the population to survive. If dispersers survive moderately well, a low dispersal rate will suffice to re-establish the empty areas without "wasting" too many dispersers



(c)

FIGURE 1 (continued)

due to disperser mortality. If disperser survival is very low a larger dispersal rate is necessary to maintain the minimal level of re-establishment of local populations, so the optimal dispersal rate increases. This prediction does not occur in the other two models because they do not directly model local extinctions.

Levin *et al.*¹⁷ (Figure 1B) produced another qualitative prediction that occurs because of their method of modeling disturbance. As the disturbance rate increases the shape of the curve changes from concave to convex. In this model disturbance represents the probability that local habitat patches have a much reduced carrying capacity (or maximum population size). As the disturbance rate increases, the availability of patches where large population growth is possible (*i.e.*, maximum population 100 times the reduced areas) decreases. In this case even if disperser mortality rate is high, the

advantages of a disperser finding one of these good patches outweighs the risk of mortality en route. This results in the convex shape of the curve (Figure 1B, dashed line).

Other Modeling Results. Venable and Brown²¹ conducted simulations of density-independent population growth to look at the interactions of dispersal, dormancy, and seed size as adaptations for reducing risk in variable environments. They used population growth rate as a measure of the fitness of a strategy. Disturbance was modeled as an array of possible environmental conditions that occurred with particular probabilities and influenced seed yield. They found that (i) if there is no temporal variance in environmental quality (*i.e.*, no disturbance), and if dispersal has some survival cost, natural selection will always operate against dispersal and (ii) conversely, if there is disturbance and dispersal has no survival cost, natural selection will always favor dispersal. However, it is likely that in most cases there is some disturbance and some cost to dispersal. For this scenario, Venable and Brown showed that optimal dispersal rate is highest for intermediate levels of disturbance. Their explanation is that the value of dispersal is in moving individuals away from unfavorable and into favorable places. This occurs less frequently as either favorable or unfavorable conditions become rare. This result is at odds with the predictions of Levin *et al.*,¹⁷ Comins *et al.*,¹⁹ and Klinkhamer *et al.*²⁰ described above, in which optimal dispersal rate is predicted to be greatest for the cases with the highest disturbance levels. The probable explanation for this difference is that the highest disturbance levels considered by Venable and Brown represented higher levels than those considered by the other authors.

Venable and Brown also showed that an increase in the number of local populations results in an increase in selection for dispersal. If the number of patches is larger, there is less year-to-year variability in the proportion of favorable patches, which means that at least some dispersers will survive. According to their model, the optimal rate of dispersal is also influenced by dispersal distance. The optimal dispersal rate declines as average dispersal distance declines, a result also reported by Palmer and Strathman.²² This is because if dispersal distance is shorter, dispersal is a less effective means of escaping from unfavorable conditions and finding favorable ones. Finally, Venable and Brown examined the effects of spatial and temporal correlation in disturbances on the evolution

of different dispersal strategies. They predicted that as the spatial correlation of disturbances increases, lower dispersal rate is favored. In this case, since most nearby patches will be either favorable or unfavorable in any given year, the effect of dispersal is to move individuals to similar patches. Since there is a cost to dispersal this will be selected against. Gadgil²³ and Klinkhamer *et al.*²⁰ also made this prediction. In addition, Venable and Brown found that increasing temporal correlation in disturbance reduces the optimal level of dispersal; as patch favorability becomes more predictable, selection favors less dispersal.

Population Stability

It is widely believed that dispersal among local populations increases the persistence time of the regional population.²⁴⁻²⁸ This is because dispersal allows re-establishment of local populations that become extinct due to factors such as disturbance.

Analytical models of population dynamics have been used to study the effects of stochastic variation in parameter values (*i.e.*, disturbance) on population survival. The effect of dispersal is then examined by comparing the case in which the population is in one uniform patch, with that in which the population is divided into local populations with dispersal among them.

May²⁹ studied the effect of stochastic variation in population growth rate, r . For the case of a single population, his analysis predicts that population survival is assured if $r > \sigma^2$, where σ^2 is the variance associated with the random fluctuations in r . For the case of many local populations, he described the dispersal process as

$$pN_{\alpha}(t+1; \text{after dispersal}) = (1/p) \sum_{\beta=1}^p N_{\beta}(t; \text{before dispersal}) \quad (3)$$

where p is the number of local populations and α and β denote local populations. May showed that the criterion for the population to persist is now $r > (\sigma^2/p)$, rather than $r > \sigma^2$ as above. The exchange of organisms among local populations is therefore pre-

dicted to average out local fluctuations over space, and enhance population survival.

Vance^{30,31} studied the effect of stochastic variation in death rate. In his model the per capita death rate in each local population is $d + \sigma_d e_i(t) + d_1 N_1$. Here, d is the mean per capita death rate, $\sigma_d e_i$ is stochastic variability in the death rate in local population i in time t , and $d_1 N_1$ is the effect of juvenile population size (N_1) on juvenile death rate (d_1). Vance found that for the case of a single population in one patch, the population variance is

$$v = \frac{N^2 \beta_d^2}{2(b-d)} \quad (4)$$

If many local populations are included, and assuming that dispersers from one local population are evenly distributed among all other local populations, the population variance is

$$v_i = \left[1 - \left(\frac{n-1}{n} \right) \left(\frac{b}{2b-d} \right) \right] \frac{N^2 \beta_d^2}{2(b-d)} \quad (5)$$

where n is the number of local populations. This is lower than the variability in the single population case, which qualitatively confirms the results of May.²⁹

Other studies, including both analytical and simulation, generally agree with the idea that dispersal improves stability of systems that are destabilized by disturbance.³²⁻³⁶ One exception to this generality appears to be Vance's finding that under some conditions of density-dependence, dispersal can destabilize populations.³¹ Vance studied a model in which disturbances cause population reductions. If juveniles disperse and individuals in small local populations have higher birth rates than those in large ones, dispersal can destabilize the population. Following a local disturbance, the local population density is low, leading to high birth rates. This leads to high dispersal rates of the young individuals (juveniles) from small populations. This increases the overall population variability, thus decreasing stability. Vance found a similar effect if adults disperse and high population growth rates cause high dispersal rates. Since population growth rate is highest at low population densities, this situation again results in high dispersal rates when population density is low.

Interestingly, Reddingius and den Boer³² reported that the re-

sponse of populations to environmental variability does not depend on whether dispersal is density-independent or density-dependent. The discrepancy between this conclusion and Vance's³¹ conclusion may be due to the fact that the two studies used different methods to model disturbance. Vance modeled local populations that experience severe reductions in numbers, whereas Reddingius and den Boer modeled disturbance by allowing model parameters to vary stochastically (positive or negative fluctuations).

How Do Disturbance Probability and Dispersal Rate Interact to Influence Regional Extinction?: A Simulation Study. Studies of the interaction between disturbance and dispersal on population stability (*i.e.*, those that I review here) take a presence/absence approach to dispersal. The question is whether and under what conditions dispersal enhances population stability. Comparisons are made of population dynamics without dispersal and with dispersal. The actual dispersal rate (fraction of individuals dispersing) used in the models varies between studies, but to date the possible effect of different dispersal rates on the model predictions has not been considered. If the qualitative effect of dispersal (*i.e.*, positive or negative) on population stability depends on the dispersal rate, then it is possible that conclusions from studies of the interaction between disturbance and dispersal could depend on the particular combinations of disturbance level and dispersal rate used in the model.

To address this problem I developed a simulation model that allowed me to simultaneously observe the effects of dispersal rate and disturbance probability on population survival. The model^{37,38} simulates the dynamics of 10 local populations. Dispersal occurs between local populations and dispersers have increased mortality, *i.e.*, there is a cost to dispersal. Each time step there is some probability that local populations can become extinct (disturbance).

I conducted 500 simulations. In each simulation a random value between 0.0 and 1.0 was chosen for the local disturbance (*i.e.*, extinction) probability (x) and another for the dispersal rate (m). Each simulation ran for a maximum of 500 time steps. If the population became regionally extinct (*i.e.*, all local populations simultaneously extinct) before completion of the 500 steps (most did), the simulation was terminated, and the time of regional extinction was recorded.

I analyzed the results of the simulations using stepwise multiple regression analysis. The dependent variable was $\ln(\text{survival time} + 1)$, and the predictor model included all first, second, and third order polynomial terms of dispersal rate (m) and disturbance probability (x) (i.e., $m, x, m^2, x^2, mx, m^3, x^3, m^2x, mx^2$).

The results, summarized in Figure 2, indicate that the effect of disturbance on population survival depends on the interaction between the disturbance probability and the dispersal rate. If disturbances (local extinctions) are frequent, high dispersal rates result in the longest survival times; regional extinction would occur quickly without dispersal. However, if disturbances are infrequent, low dispersal rates result in the longest survival times. Low dispersal rates are sufficient to replenish extinct local populations, whereas if the dispersal rate is too high the cost of dispersal outweighs the benefit of recolonization, and the net effect is a reduction in survival time. For intermediate disturbance probabilities, moderate dispersal rates result in the longest survival times.

The results are significant because they suggest that whether dispersal increases or decreases population stability depends on

the disturbance probability and the dispersal rate. Also, the results are important because they contrast with some of the predictions from the studies of individual selection on disturbance reviewed above. In these evolutionary analyses dispersal is always given some selective advantage no matter how low the disturbance level, as long as there is some probability of disturbance¹⁷ (although see Horvitz and Schemske³⁹). In contrast, my simulations predict that at low disturbance levels even low dispersal rates can reduce population survival. A second contrasting result from individual selection is the result of Venable and Brown²¹ that the optimal dispersal rate is highest for intermediate disturbance levels. In contrast, my results predict that the stabilizing effect of dispersal (i.e., relative increase in survival time) is greatest for the highest disturbance levels. In this case the difference between the predictions cannot be due to my choice of disturbance levels, since my simulations include the complete possible range. These contrasting results between individual selection and population stability lead to the suggestion that natural selection may often favor dispersal rates that do not produce the most stable population dynamics.

Disturbance Size. Coffin and Lauenroth⁴⁰ conducted simulation experiments of the disturbance-driven population dynamics of the grass species, blue grama (*Bouteloua gracilis*). They used a spatially explicit model in which local grass populations could be destroyed by disturbance. Seeds could disperse a certain distance from their source plot. As they increased the size of the disturbance, the recovery time of the population increased. This is because the central part of a large disturbed area is too far from potential sources of colonists to be quickly re-established; re-establishment in these central areas does not occur until after the outer parts are first re-colonized.

Some Other Issues

Number of Local Populations. Agur and Deneubourg³⁶ predicted a large increase in survival time with increasing number of local populations. In their simulations the local extinction probability and the total regional carrying capacity were held constant, while the habitat was subdivided into more and more habitat patches.

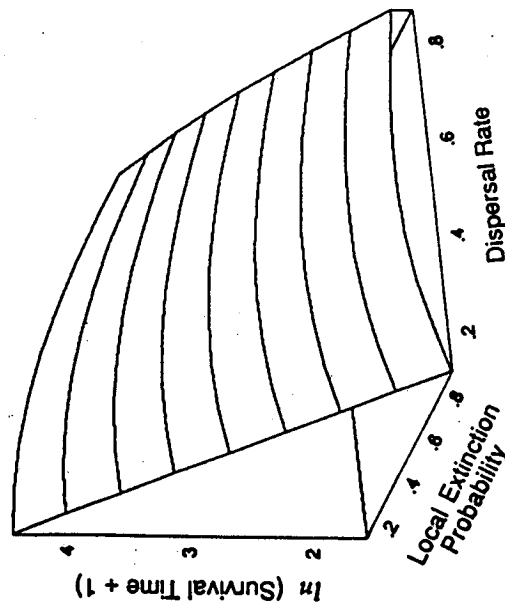


FIGURE 2. Interacting effects of dispersal rate and disturbance frequency (local extinction probability on $\ln(\text{survival time} + 1)$) from simulation experiments.

As the habitat becomes more subdivided, it becomes less likely that all or most patches will experience a disturbance simultaneously, which increases the overall survival time. Roff¹¹ reported a similar result with the same explanation. He found that mean local population size increased with increasing number of patches up to a maximum of between 15 and 25 patches.

Dispersal Corridors. There are two common methods for modeling dispersal. The first is to assume that all dispersers have equal access to all patches. The second assumes that dispersers can only disperse to neighboring patches. Roff¹¹ and Vance¹² compared results of population size and stability for these two assumptions. Both found that there was very little qualitative difference between the predictions, although quantitatively the assumption of equal access tends to overestimate the effect of dispersal on the population.

A third method of modeling dispersal is to assume that some habitat patches are connected to others by means of "dispersal corridors." Lefkovich and Fahrig¹³ used this dispersal assumption in a model of mice in patches of woods that may or may not be connected by wooded fencerows along which dispersing mice travel. The disturbance in this model is produced by the combination of stochastic parameter values in the model, and a yearly winter mortality rate of 85%. It was found that in this model, the specific way in which the patches are connected affects the survival time of local and regional populations. The most important factor determining the survival time of a local population is the largest geometric figure (*i.e.*, the figure having the largest number of sides) of which the patch forms a part. This result is illustrated in Figure 3. In this figure, the local population in patch *a* has an increasing probability of survival as one moves from Figure 3A to 3B to 3C. At first this seems counterintuitive because *a* has fewer dispersal corridors to other patches in the successive scenarios. However, the largest geometric figure of which *a* is a part increases from a line (3A) to a triangle (3B) to a pentagon (3C). The explanation for this finding can be best understood by comparing Figures 3A and 3C. In Figure 3A, if *a* goes extinct in one time step, the other four patches have no source of colonists. This can easily lead to regional extinction if *a* is not quickly replenished sufficiently to be able to in turn replenish other patches that may be empty or have low populations. This scenario is in contrast with the situation depicted in Figure 3C. Here it would be necessary

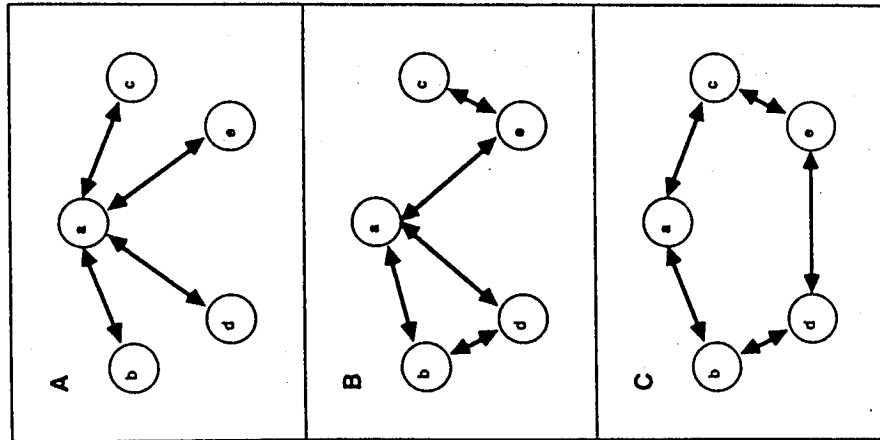


FIGURE 3 Three hypothetical spatial arrangements of five habitat patches (a-e). Circles represent patches and double-headed arrows represent connections between patches along which dispersing individuals can travel. Local and regional population survival time increases from scenarios A to C.

for all patches to become simultaneously extinct to produce a regional extinction.

SUMMARY OF THEORETICAL RESULTS

Individual Selection

- 1) High disturbance frequency leads to selection for dispersal.^{2,14,15,17,19,20}

- 2) Optimal dispersal rate increases with increasing number of local populations.²¹
- 3) Optimal dispersal rate is highest at intermediate levels of disturbance.²¹
- 4) Optimal dispersal rate decreases with increasing spatial correlation in disturbances.²⁰⁻²³
- 5) Optimal dispersal rate decreases with increasing temporal correlation in disturbances.²¹
- 6) Optimal dispersal rate decreases with decreasing dispersal distance.^{21,22}

Population Stability

- 1) Dispersal acts to increase population stability by decreasing the effects of disturbance,^{29-33,35,36} unless
 - (i) dispersal rate is highest at low population densities³¹ (*i.e.*, there is inversely density-dependent dispersal), or
 - (ii) disturbance level is low (my results above).
- 2) As disturbance size increases population stability decreases for constant dispersal distance.⁴⁰
- 3) Increasing the number of local populations increases overall population stability.^{36,41}
- 4) The spatial pattern of dispersal corridors can affect overall population stability.⁴²

EMPIRICAL STUDIES

Dispersal Strategies. There is some evidence that dispersal strategies evolve as predicted by the theories. In plants, production of seeds with adaptations for dispersal—small size and special morphological design—is correlated with a fugitive species' ability to respond to large disturbances.^{43,44} Denno⁴⁵ has shown a relationship between the frequency of winged individuals in populations of leafhoppers, and habitat disturbance frequency.

Whereas the theoretical work has focussed almost exclusively on dispersal rate, many empirical studies have considered relationships between disturbance and optimal dispersal distance. For

example, the mean dispersal distance of six species of prairie plants is correlated with the mean distance between optimal habitats created by disturbance.⁴⁶ Similarly, Howe and Smallwood⁴⁴ showed that dispersal distances of seeds from fugitive plants are greater than for non-fugitives. For plants colonizing areas disturbed by badgers in tall-grass prairie, Platt⁴⁷ reported a correlation between inter-disturbance distance and dispersal distance. Finally, Ellner and Schmid⁴⁸ argue that desert annuals have low dispersal distances in part because of the relatively low spatio-temporal variability in deserts within feasible dispersal ranges.

Population Dynamics. The importance of disturbance for insect population dynamics is well recognised. Dempster and Pollard⁴⁹ state that for many if not most insects, population fluctuations due to direct and indirect effects of environmental conditions (mainly weather) are more important than interactions with other species. (Although several workers studying host-parasitoid systems have disputed this claim, *e.g.*, Hassell and May⁵⁰). In addition, for some insect species, local extinctions are common events and populations depend on dispersal among local populations to avoid regional extinctions.^{26,51-53} Relationships between dispersal rates and population stability have also been noted for mesquite,⁵⁴ tropical trees,⁵⁵ and forest gastropods.⁵⁶

The question of how dispersal corridors between local habitats affect the relationship between dispersal, disturbance and population stability is still largely unknown. Fahrig and Merriam³⁸ showed that for populations of white-footed mice, dispersal corridors can be important in determining which local populations have a high potential for recolonization and therefore a high survival probability.

FUTURE DIRECTIONS

The main impediments to the emergence of a well-integrated body of ecological disturbance theory are (i) a lack of recognition that "variability" in population studies is synonymous with "disturbance" in ecosystem studies and (ii) a lack of integration of theories related to variability across spatial and temporal scales into the single topic of "disturbance ecology." As a starting point to the

solution researchers should adopt a common less system- or tradition-oriented definition of disturbance. An appropriate candidate for such a definition is the one suggested by Rykiel: to paraphrase, a disturbance is an external force that causes a detectable perturbation of an ecological system.

Empirical Directions

Most of the hypotheses generated in the theoretical literature depend on the assumption that there is a significant cost to dispersal. In the case of animal populations, it is assumed that dispersal takes more energy and exposes the animal to higher risk of predation than would be experienced if it remained at its home patch. However, due to the difficulty of obtaining relative estimates of survival rates of individuals that disperse and those that do not, there is little or no information to support this assumption. In the case of plants, there is evidence that the survival rate of dispersing seeds is often actually higher than the survival rate of seeds that fall near the parent plant (e.g., Augspurger⁵⁵). Theories that assume cost to dispersal may not be applicable to these cases. Therefore, empirical studies of the cost of dispersal in natural populations are critical for establishing the potential range of applicability of the theoretical results reviewed here.

For several of the hypotheses that have been proposed there are no field data against which they can be compared. These include the hypotheses that optimal dispersal rate is highest at intermediate levels of disturbance, and optimal dispersal rate decreases with increasing spatial and temporal correlations in disturbances, or with decreasing dispersal distance. It is also unknown whether the conditions proposed by Vance³¹ in which dispersal destabilizes population dynamics occur in nature, and whether dispersal destabilizes populations when the disturbance rate is low.

Theoretical Directions

Several authors have noted that any particular disturbance regime has many identifiable characteristics, including disturbance intensity, frequency, spatial extent and duration.^{1,3,57,58} It would be interesting to see how variation in these factors affects the theoretical

predictions about disturbance and dispersal. This level of detail will require that theoretical ecologists increasingly use simulation models to make predictions. There is an urgent need for the development of systematic methods for examining the results of such simulations so that general hypotheses can be formulated.⁵⁸

In this paper I have limited my review to studies of single species. However, much of the theoretical work that deals with disturbance focuses on the combined effects of disturbance and competition. For example, Chesson⁵⁹ showed that variability in birth rates can promote coexistence of competing species by ensuring that each species has periods in which it is increasing. Chesson and Huntly⁶⁰ studied the effect of covariance between the probability of favorable environmental conditions at an early life history stage with the intensity of competition at a later stage. They found that whether disturbance promotes or demotes coexistence depends on how the growth rate responds to the joint effects of disturbance and competition. Chesson¹¹ also showed that variation in death rates may either promote or demote coexistence depending on the circumstances. Ultimately we need to synthesize the results of disturbance and dispersal theory from single species models with community level analyses such as those of Chesson. It will be particularly interesting to learn whether results concerning the likelihood of extinction for single species carry over to communities.

Finally, it is clear that many of the theoretical predictions about disturbance and dispersal depend on the methods used for modeling disturbance. This presents a challenge to theoreticians: it would be useful if different kinds of disturbances could be grouped into categories that are meaningful in terms of their qualitative effects on individual selection and population stability. To do this effectively, theoreticians will need to become better informed of relevant field studies so that they will have a better appreciation of the characteristics of natural disturbances.

Acknowledgments

I would like to thank Peter Kareiva for his detailed, constructive criticisms of the manuscript. I am also grateful to Dean Urban, Ed Rykiel and two anonymous reviewers for their comments. This work was supported by NSF LTER grant BSR8702333.

LENORE FAHRIG

Department of Fisheries and Oceans
Science Branch
P.O. Box 5667
St. John's Newfoundland
Canada A1C 5X1

References

1. E. J. Rykiel, Jr., *Austr. J. Ecol.* **10**, 361 (1985).
2. J. P. Grime, *Plant Strategies and Vegetation Processes*, (Wiley, Chichester 1979).
3. W. P. Sousa, *Ann. Rev. Ecol. and Systematics* **15**, 353 (1984).
4. J. R. Karr and K. E. Freemark, in *The Ecology of Natural Disturbance and Patch Dynamics*, eds. S. T. A. Pickett and P. S. White, (Academic Press, New York 1985).
5. P. S. White and S. T. A. Pickett, in *The Ecology of Natural Disturbance and Patch Dynamics*, eds. S. T. A. Pickett and P. S. White, (Academic Press, New York 1985).
6. D. L. DeAngelis, C. C. Travis and W. M. Post, *Theor. Pop. Biol.* **16**, 107 (1979).
7. P. Kareiva, in *Community Ecology*, eds. J. Diamond and T. Case, (Harper and Row, New York 1985).
8. H. A. Mooney and M. Godron, eds., *Disturbance and Ecosystems*, (Springer-Verlag, New York 1983).
9. S. T. A. Pickett and P. S. White, eds., *The Ecology of Natural Disturbance and Patch Dynamics*, (Academic Press, New York 1985).
10. M. Turelli, *Theor. Pop. Biol.* **12**, 140 (1977).
11. P. L. Chesson, *Theor. Pop. Biol.* **28**, 263 (1985).
12. R. M. May, *Stability and Complexity in Model Ecosystems: Monographs in Population Biology No. 6*, (Princeton University Press, Princeton 1973).
13. W. P. Sousa, in *The Ecology of Natural Disturbance and Patch Dynamics*, eds. S. T. A. Pickett and P. S. White, (Academic Press, New York 1985).
14. R. H. MacArthur and E. O. Wilson, *The Theory of Island Biogeography*, (Princeton University Press, Princeton 1967).
15. P. J. den Boer, *Acta Biotheoretica* **18**, 165 (1968).
16. E. Holm, *Oecologia* **75**, 141 (1988).
17. S. A. Levin, D. Cohen and A. Hastings, *Theor. Pop. Biol.* **26**, 165 (1984).
18. J. Maynard Smith, *Ann. Rev. Ecol. Systematics* **9**, 31 (1978).
19. H. N. Comins, W. D. Hamilton and R. M. May, *J. Theor. Biol.* **82**, 205 (1980).
20. P. G. L. Klinkhamer, T. J. deJong, J. A. J. Metz and J. Val, *Theor. Pop. Biol.* **32**, 127 (1987).
21. D. L. Venable and J. S. Brown, *Amer. Naturalist* **131**, 360 (1988).
22. A. R. Palmer and R. R. Strathman, *Oecologia* **48**, 308 (1981).
23. M. Gadgil, *Ecology* **52**, 253 (1971).
24. D. L. DeAngelis, C. C. Travis and W. M. Post, *Theor. Pop. Biol.* **16**, 107 (1979).
25. A. Lomnicki, *Oikos* **35**, 185 (1980).
26. P. J. den Boer, *Oecologia* **50**, 39 (1981).
27. A. Hastings, *J. Math. Biol.* **16**, 49 (1982).
28. L. Fahrig and G. Merriam, *Ecology* **66**, 1762 (1985).
29. R. M. May, in *Progress in Theoretical Biology*, eds. R. Rosen and R. M. Snell, (Academic Press, London 1974).
30. R. R. Vance, *Theor. Pop. Biol.* **18**, 343 (1980).
31. R. R. Vance, *Amer. Naturalist* **123**, 230 (1984).
32. J. Reddingius and P. J. den Boer, *Oecologia* **5**, 240 (1970).
33. D. A. Roff, *Oecologia* **15**, 245 (1974).
34. I. Hanski, *Ecology* **66**, 335 (1985).
35. E. Kuno, *Oecologia* **49**, 123 (1981).
36. Z. Agur and J. L. Deneubourg, *Theor. Pop. Biol.* **27**, 75 (1985).
37. L. Fahrig, *Appl. Math. Computation* **27**, 53 (1988).
38. L. Fahrig and J. Paloheimo, *Theor. Pop. Biol.* **34**, 194 (1988).
39. C. C. Horvitz and D. W. Schemske, in *Fragivores and Seed Dispersal*, eds. A. Estrada and T. H. Fleming, (Dr. W. Junk, Dordrecht 1986).
40. D. P. Coffin and W. K. Lauenroth, *Landscape Ecology*. In press (1989).
41. D. A. Roff, *Oecologia* **15**, 259 (1974).
42. L. P. Lefkovich and L. Fahrig, *Ecol. Mod.* **30**, 297 (1985).
43. H. G. Baker, *Ann. Rev. Ecol. Systematics* **5**, 1 (1974).
44. H. F. Howe and J. Smallwood, *Ann. Rev. Ecol. Systematics* **13**, 201 (1982).
45. R. F. Denno, in *Migration: mechanics and adaptive significance*, ed. R. A. Rankin, (Marine Science Institute, Port Arkansas, Texas 1985).
46. K. Rice and S. Jain, in *The Ecology of Natural Disturbance and Patch Dynamics*, eds. S. T. A. Pickett and P. S. White, (Academic Press, New York 1985).
47. W. J. Platt, *Ecol. Monographs* **45**, 285 (1975).
48. S. Ellner and A. Shmida, *Oecologia* **51**, 133 (1981).
49. J. P. Dempster and E. Pollard, *Oecologia* **50**, 412 (1981).
50. M. P. Hassell and R. M. May, *Annales Zoologicae Fennicae* **25**, 55 (1988).
51. P. R. Ehrlich, R. R. White, M. C. Stinger, S. W. McKechnie and L. E. Gilbert, *Science* **188**, 221 (1975).
52. E. F. Connor, S. H. Faeth and D. Simberloff, *Ecology* **64**, 191 (1983).
53. C. Solbreck and B. Silen-Tullberg, *Oecologia* **71**, 51 (1986).
54. J. R. Brown and S. Archer, *Vegetatio* **73**, 73 (1987).
55. C. K. Augspurger, *Oikos* **40**, 189 (1983).
56. D. Strayer, S. P. Hamburg, S. C. Nodvin and D. H. Pletscher, *Can. J. Zoology* **64**, 2094 (1986).
57. F. A. Bazzaz, in H. A. Mooney and M. Godron, eds., *Disturbance and Ecosystems*, (Springer-Verlag, New York 1983).
58. L. Fahrig, in *Quantitative Methods for Landscape Ecology*, eds. M. G. Turner and R. H. Gardner. In press. (Springer-Verlag, New York 1990).
59. P. L. Chesson, *J. Math. Biol.* **15**, 1 (1982).
60. P. Chesson and N. Huntly, *Annales Zoologicae Fennicae* **25**, 5 (1988).