

A PATCH MODELING APPROACH TO THE COMMUNITY-LEVEL CONSEQUENCES OF DIRECTIONAL DISPERSAL

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Abstract. Although plants and other sessile organisms often disperse in a prevailing direction, the ecological consequences of this are poorly understood. To explore patterns of plant diversity similar to those found in a California river system, I modeled perennial plant populations and communities occurring in a linear series of neighborhoods connected by dispersal, where dispersal occurs in a prevailing downstream direction. Simulations demonstrated that population size and species diversity correlated with dispersal and increased downstream, but only if fecundity and death rates were such that neighborhoods within the system depended on external propagule input for their persistence. Highly effective downstream dispersal and some upstream dispersal were also required. If these demographic and dispersal criteria were met, communities with intense competition and inhibition still developed downstream increases in diversity. Additionally, in such systems, directional dispersal could favor species coexistence since upstream neighborhoods provided a refuge for inferior competitors. The demographic and dispersal criteria were relaxed for systems recovering from scattered source populations following disturbance. I conclude that directional dispersal may be a key determinant of species coexistence and patterns of diversity in severely propagule-limited systems.

Key words: *coexistence; community; directional dispersal; disturbance; patch model; river; species diversity.*

INTRODUCTION

Ecologists have long appreciated the importance of dispersal for the spread and persistence of populations (Skellam 1951, Harper 1977). More recently, increased attention to spatial processes, more detailed examination of dispersal distance, and mounting evidence for dispersal limitation, have generated a surge of interest in how spatial patterns of dispersal influence patterns of community structure (Tilman and Kareiva 1997, Clarke 1998, Nathan and Muller-Landau 2000, Levine 2001, Wang and Smith 2002). A number of theoretical studies have examined the conditions under which local and long-distance dispersal influence species coexistence, diversity, species–area relationships, and relative abundance patterns (Holmes and Wilson 1998, Bolker and Pacala 1999, Stoll and Prati 2001, Chave et al. 2002). Nearly all of this literature, however, has focused on only one component of the dispersal pattern, the distance over which propagules move away from the source (Fig. 1A). Far less explored are population and community-level consequences of propagule transport in a prevailing direction (Fig. 1B).

Directional dispersal is an obvious feature of many natural systems. Waterborne seeds and aquatic organisms in rivers flow primarily downstream (Waser et al. 1982, Speirs and Gurney 2001), and planktonic larvae in marine

systems usually disperse with prevailing long-shore currents (Roughgarden et al. 1988). Animals often move seeds towards particular locations (Harper 1977) and wind, the major dispersal agent for plants, often blows in one direction. Although the problems directional dispersal poses for population persistence are well appreciated (Anholt 1995, Speirs and Gurney 2001), directional dispersal may also influence community structure. In metapopulation (Levins 1969, Hanski and Gilpin 1997), spatial mass effect (Shmida and Ellner 1984), source-sink (Eriksson 1996), and lottery (Chesson and Warner 1981) systems, spatial variation in the supply of propagules, as might result from directional dispersal, can influence community patterns. Better understanding this influence is important for predicting the rates at which exotic species spread, the ability of species to move with changing climates, and the ecological impacts of human-caused alteration of dispersal vectors.

In this paper, I use simulation models to explore the dynamics of populations and communities in systems where dispersal occurs in a prevailing direction. The model is based on the plant community occurring along the South Fork Eel River in California (Levine 2000a, b, 2001). River systems such as the Eel provide an ideal habitat in which to examine the community-level consequences of directional dispersal because, not only do water and waterborne seeds move unidirectionally downstream, but plants in these systems are linearly arrayed along the channel. This one-dimensional nature simplifies the mathematical formulation of models and the assessment of the spatial patterns that develop.

Past work in the Eel River system suggests an important role for directional dispersal in driving community patterns. The diversity of plants living on small (400 cm²) sedge tussock islands more than doubles with

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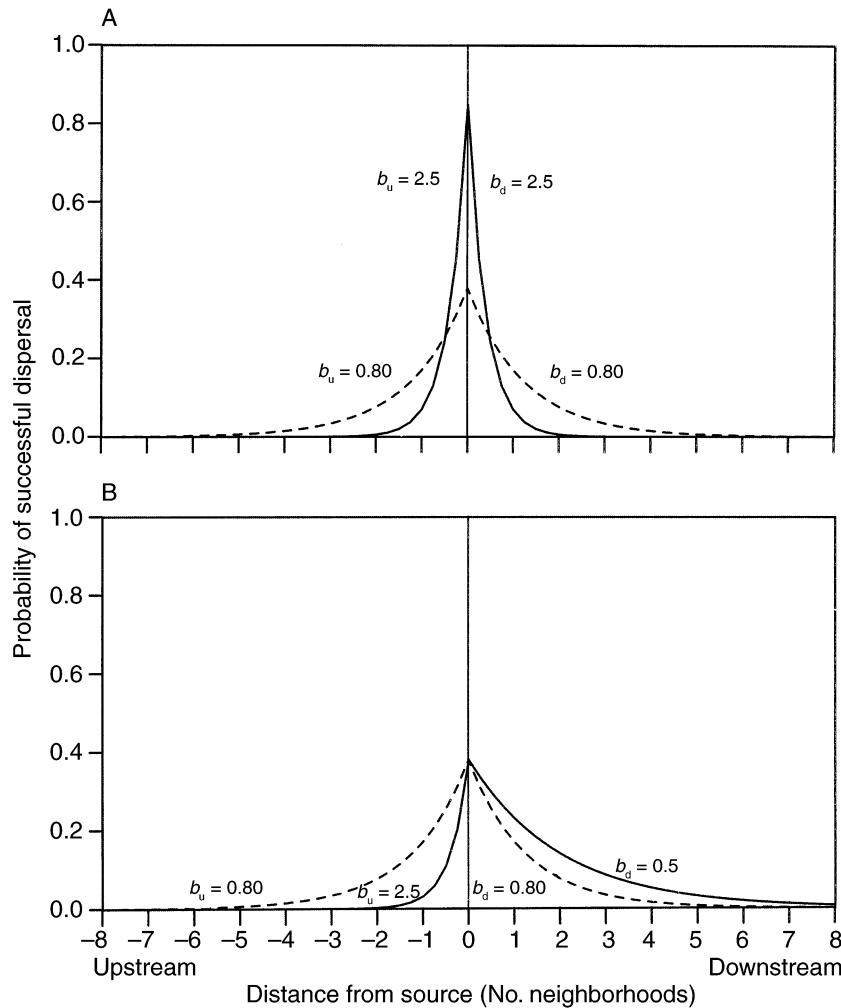


FIG. 1. Negative exponential dispersal kernels where (A) the overall effectiveness and (B) the prevailing direction of dispersal vary. The upstream and downstream dispersal parameters from a negative exponential model of dispersal are b_u and b_d (see Eq. 2).

distance downstream over the 8 km study stretch (Levine 2000a, 2001). More specifically, all of these species are found throughout the study system growing almost exclusively on sedge islands (Levine 2000b), but are concentrated on the downstream tussocks. Seed addition experiments demonstrate an important role for propagule supply in contributing to these patterns (Levine 2001). Similar downstream increases in diversity have been found for plants (Nilsson et al. 1994, Pollock et al. 1998, Honnay et al. 2001) and aquatic invertebrates (Grubaugh et al. 1996, Vinson and Hawkins 1998, Wiberg-Larson et al. 2000) over stretches of other river systems. That patterns such as these are the product of directional dispersal is often regarded as commonsensical (Friedman and Stein 1980, Honnay et al. 2001). In this paper, however, I demonstrate that this intuitive notion is too simple.

Here, I present multispecies Markov chain models describing the dynamics of species occurring in a linear series of habitats connected by dispersal (Fig. 2). I use

these models to evaluate three interrelated questions. First, what are the demographic and dispersal traits required for directional dispersal to drive patterns of population size and diversity? Second, how do species interactions and system-wide disturbance influence these criteria? Third, how does directional dispersal influence species coexistence?

SINGLE-SPECIES AND NONINTERACTIVE MULTISPECIES SYSTEMS

Patch models are well suited to describing the dynamics of the numerous herbaceous perennial plants in the Eel River system, because these species are found in discrete patches of habitat at two spatial scales. At the broader scale, the plants occur primarily in riffles, the discrete cascading sections of river separated by long quiet stretches of water. At the finer scale within each riffle, plants grow almost exclusively on tussock vegetation islands formed by the sedge, *Carex nudata* (Levine 2000b). The model system is thus a linear series of neighborhoods

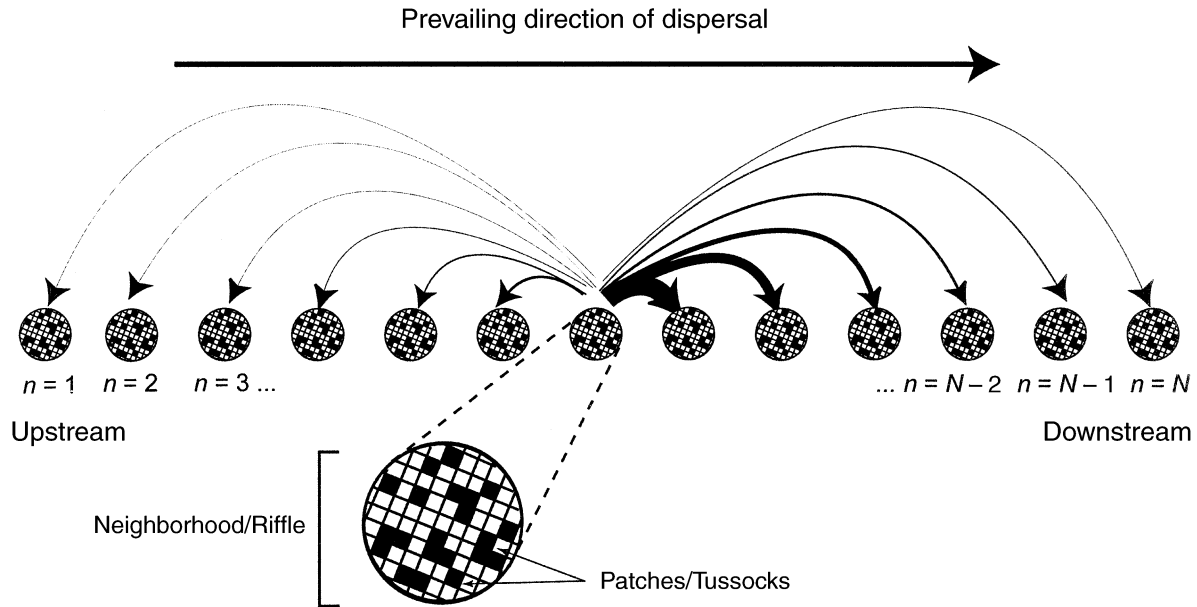


FIG. 2. Diagram of the model system showing a linear series of neighborhoods, each composed of numerous patches. With respect to the Eel River plant community, the neighborhoods (the circles) are analogous to the riffles and the patches (the squares) to the tussocks.

corresponding to the riffles; each composed of numerous patches corresponding to tussocks (Fig. 2). Although the term neighborhood is often used to define the scale of species interactions, here I use neighborhood simply to mean a collection of nearby patches or tussocks as one finds at a riffle.

Model structure

For a single-species model, each occupied patch contains a single plant. When it dies, the patch (tussock) becomes unoccupied and stays in that state until a colonist arrives. Thus, the dynamics of empty and occupied patches within a given neighborhood (riffle) j can be described by the matrix format Markov chain:

$$\begin{bmatrix} 1 - P \\ P \end{bmatrix}_{j,t+1} = \begin{bmatrix} (1 - C_j) & D(1 - C_j) \\ C_j & 1 - D + DC_j \end{bmatrix} \times \begin{bmatrix} 1 - P \\ P \end{bmatrix}_{j,t} \quad (1)$$

where P is the proportion of occupied patches within neighborhood j , and D is the death rate. C_j is the probability a patch in neighborhood j is colonized—a function of fecundity and patch occupancy (see Eq. 2 below). C_j is the same for all patches in neighborhood j , and thus within neighborhoods, space is implicit, and all patches are equally likely to be colonized by any other. The model is presented as a Markov chain because the format is conducive to the multispecies extensions described below (Caswell and Cohen 1991).

Following the Eel River plant system, the time step begins at the end of the growing season after seeds or

other propagules have been released, but before the winter floods that kill individuals. The model assumes that death, colonization, competition, and seed production and dispersal then occur in the aforementioned order and do not overlap. Thus a patch can lose its plant to disturbance but be recolonized within the time step (hence DC_j in element 2,2). Also assumed is an infinite number of patches in all neighborhoods, though results are unchanged in stochastic simulations where similar to the Eel system, patches contain 100 neighborhoods, and colonization and death are random.

The full model tracks the proportion of occupied patches in a linear series of N total neighborhoods (riffles), with neighborhood N representing the patch furthest downstream (Fig. 2). The model is thus a system of N equations, each describing the dynamics of a neighborhood according to Eq. 1, and coupled through colonization. C_j , the probability that a given patch in neighborhood j receives at least one propagule, is 1 minus the probability that no propagules arrive:

$$C_j = 1 - \exp \left\{ - \sum_{n=1}^{j-1} fP_{n,t} \frac{\exp[-b_d(j-n)]}{k} - \sum_{n=j}^N fP_{n,t} \frac{\exp[-b_u(n-j)]}{k} \right\} \quad (2)$$

$$k = \frac{e^{-b_d}}{1 - e^{-b_d}} + \frac{1}{1 - e^{-b_u}} \quad (3)$$

Assuming Poisson dispersal, the probability of zero arriving propagules is the negative exponential of the expected number of colonists contributed by each neighborhood n , summed over the N neighborhoods.

The contribution to patches in neighborhood j from those in neighborhood n is the product of the proportion of occupied neighborhoods in n ($P_{n,i}$), the colonists produced per occupied neighborhood (f), and the probability a propagule produced in neighborhood n disperses to neighborhood j . Specifically, we assume that dispersal follows a negative exponential model (Willson 1993), where b_u and b_d describe the rate at which upstream and downstream dispersal decline with distance from the source (Fig. 1B), $j - n$ or $n - j$ is the distance between the neighborhoods, and k scales the exponential functions so that the summed probability of dispersal to all neighborhoods in an infinitely long system is 1. The overall form of this colonization equation is similar to that used by Hanski and Ovaskainen (2000) to describe metapopulation dynamics in fragmented landscapes, and assumes no threshold distance of seed dispersal.

This single-species model also describes the dynamics of a multispecies noninteractive system composed of S identical species. In such systems, patches can contain more than one species, and the ability of species to occupy patches and produce seeds is independent of the presence of other species. For a noninteractive system of S identical species each occupying a proportion P of the patches in a given neighborhood, the mean patch richness for the neighborhood (α) is PS . Thus for noninteractive systems, I present population size and diversity results on the same plots.

Models were simulated in R version 1.2 (R Project for Statistical Computing)² for 100 years, enough time for the dynamics to stabilize. If, at this point, <0.001 of the patches in a neighborhood were occupied by a given species, it was considered extinct in the neighborhood. The simulated system is a linear array of 30 neighborhoods occupied by 30 species where the initial conditions place each species in a small fraction (0.01) of patches within each neighborhood. The boundary conditions are such that an additional neighborhood exists upstream and downstream of the system. At each time step, the proportion of occupied patches in the two boundary neighborhoods is set equal to the adjacent neighborhood.

Single species and noninteractive community results

Fecundity and death rates strongly influenced the degree to which population size and species diversity spatially tracked the direction of dispersal. If f , the fecundity rate, was 1.50, much greater than the death rate of 0.25, then the proportion of occupied patches was high in all neighborhoods (Fig. 3A). In addition, even though dispersal was strongly biased in the downstream direction, patch occupancy rates in upstream vs. downstream patches differed only marginally. Conversely, if the fecundity rate was 0.10, less than the death rate, all populations went extinct. The steepest downstream gradients (used here to mean the difference

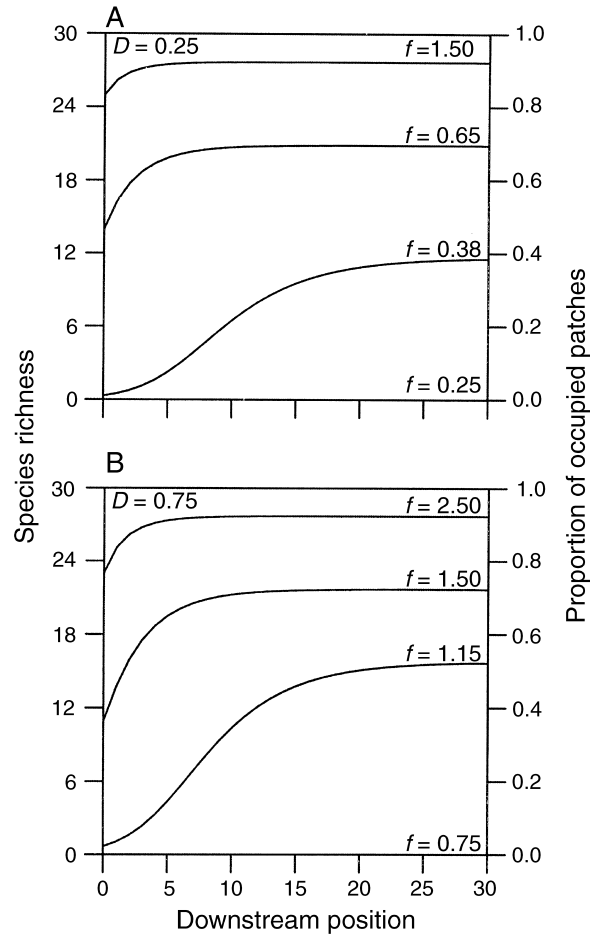


FIG. 3. Downstream gradients in species diversity and population size for a noninteractive community after 100 time steps with death rates (D) of (A) 0.25 and (B) 0.75. Each plot shows the effects of varying the fecundity term f . Dispersal follows the solid line in Fig. 2 ($b_u = 2.5$, $b_d = 0.5$).

in diversity or patch occupancy at the downstream vs. upstream ends of the gradient) in the abundance of a single species and the diversity of a multispecies system occurred when patches were dependent on external input for persistence. With an annual death rate of 0.25, the steepest downstream gradients in diversity were observed with fecundity $f = 0.38$ (Fig. 3A). With $b_u = 2.5$ and $b_d = 0.5$, k is 2.63 (Eq. 3), and thus neighborhoods retain only $1/k$ or 0.38 of the propagules they produce (Fig. 1B). This makes the effective fecundity of an isolated neighborhood $(0.38)(0.38) = 0.144$, less than the death rate of 0.25. Indeed, populations with these parameters go extinct in isolated neighborhoods. However, with other neighborhoods in the system, these propagules are not lost, but rather land in other suitable sites, which in turn disperse a fraction of their propagules to the source neighborhood. Thus, the systems in which downstream patterns of dispersal drive patterns in diversity are those where neighborhoods rely on the presence of other neighborhoods for per-

² URL: <http://www.r-project.org/>

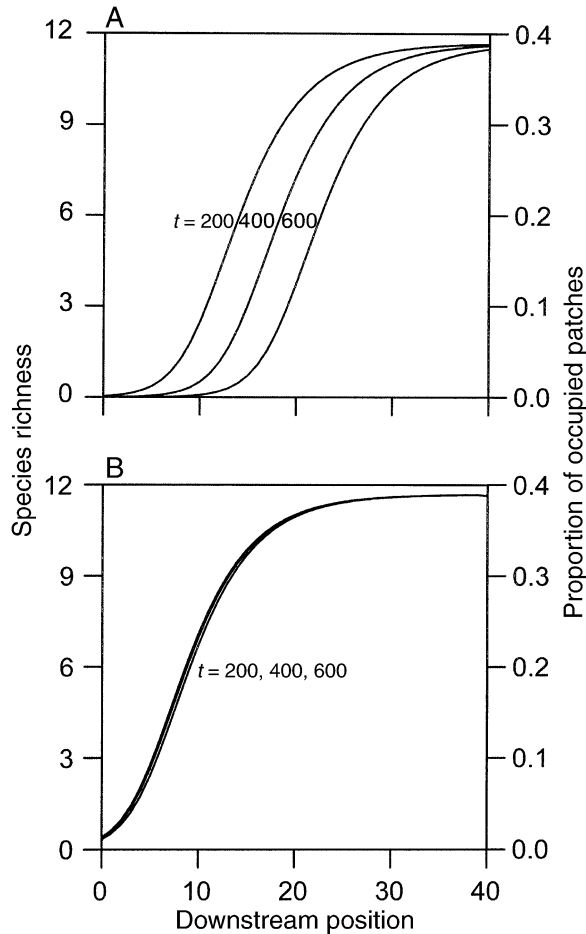


FIG. 4. Downstream gradients in species diversity and population size for a noninteractive community after 200, 400, and 600 years with and without upstream dispersal ($f = 0.38$, $D = 0.25$). (A) Dispersal is entirely downstream ($b_u = \infty$, $b_d = 0.5$). (B) Propagules have some capacity to move upstream ($b_u = 2.5$, $b_d = 0.5$). Note that the system contains 40, not 30, neighborhoods.

sistence. For a death rate of 0.75, a fecundity rate of 1.15 generates the steepest downstream population size and diversity gradients (Fig. 3B), and again the populations are dependent on external supply.

Such strict criteria are necessary because a long series of downstream dispersing patches fails to produce significant variation in the number of arriving propagules after the first or second patch. Assuming that species are uniformly distributed through a 30-patch system and that downstream dispersal follows the solid line in Fig. 1B, the 15th patch receives only 5% more propagules than the fifth. For these differences to drive long-term downstream increases in population size or diversity, the system must contain patches that are severely propagule limited. For similar reasons, the model only applies to systems near a spatial boundary. For natural analogues this may be plants occurring in a

forest fragment or those restricted to a specific geologic substrate or isolated reserve.

The importance of upstream and long-distance dispersal

The steepest downstream gradients in Fig. 3 can be regarded as standing waves anchored by upstream dispersal. Without upstream dispersal, the system behaved as a moving wave (Fig. 4A). Specifically, a spatial gradient in population size and diversity developed and then moved downstream through the system. The most upstream neighborhoods were always going extinct, cutting off dispersal to those immediately downstream and thereby driving the wave in the downstream direction. In contrast, when the model was run with some upstream dispersal ($b_u = 2.5$), the most upstream neighborhoods persisted and the wave was fixed in space (Fig. 4B). More generally, a moving wave solution to the model emerged whenever upstream dispersal was not effective enough to make the most upstream neighborhoods viable, a result more generally described by Speirs and Gurney (2001).

Highly effective long-distance dispersal was also required to produce long-term downstream increases in population size and diversity. In the Figs. 3 and 4 simulations, species disperse over one-third of their propagules to patches two or more neighborhoods away in the downstream direction. Assuming that neighborhoods are separated by 100 m or more, dispersal usually drops off much faster when moving away from the source in other systems (Harper 1977, Willson 1993). To examine a system with a more typical dispersal kernel, I ran simulations where $b_u = 5$, and $b_d = 2.25$. With these parameter values, species still disperse 17 times more propagules downstream than upstream, but overall, between-neighborhood dispersal is one-sixth as effective. With this less efficient dispersal, regardless of the fecundity rate, sizeable downstream gradients in population size and species diversity failed to develop (Fig. 5).

MULTISPECIES INTERACTIVE MODELS

To assess the relationship between species interactions and directional dispersal, I constructed multispecies models with competition and inhibition. This choice of interaction is based on past work in the Eel system (Levine 2000b). Several previous studies have added multiple competitors to a Levins (1969)-type patch model (Hastings 1980, Nee and May 1992, Tilman 1994), and here I follow the Markov chain approach presented by Caswell and Cohen (1991).

Expanding the single-species model (Eq. 1) to include two species requires expanding the number of patch states to four: neither species present (P_0), species 1 present (P_1), species 2 present (P_2), and both species present (P_{12}). For a two-species model with both inhibition I and competitive displacement X , the within neighborhood dynamics can be described by the following model (modified from Caswell and Cohen 1991):

$$\begin{bmatrix} P_e \\ P_1 \\ P_2 \\ P_{12} \end{bmatrix}_{t+1} = \mathbf{A} \begin{bmatrix} P_e \\ P_1 \\ P_2 \\ P_{12} \end{bmatrix}_t \tag{4}$$

$$\mathbf{A} = \begin{bmatrix} (1 - C_1)(1 - C_2) & D_1(1 - C_1)(1 - C_2) & D_2(1 - C_1)(1 - C_2) & D_1D_2(1 - C_1)(1 - C_2) \\ C_1(1 - C_2) & (1 - C_2I_1)(1 - D_1) + D_1C_1(1 - C_2) & C_1D_2(1 - C_2) & D_2(1 - D_1)(1 - C_2I_1) + D_2D_1C_1(1 - C_2) + (1 - D_1)(1 - D_2)X_1 \\ C_2(1 - C_1) & D_1C_2(1 - C_1) & (1 - D_2)(1 - C_1I_2) + D_2C_2(1 - C_1) & D_1(1 - D_2)(1 - C_1I_2) + D_1D_2C_2(1 - C_1) \\ C_1C_2 & (C_2I_1)(1 - D_1) + D_1C_1C_2 & (1 - D_2)(C_1I_2) + D_2C_1C_2 & (1 - D_1)(1 - D_2)(1 - X_1) + D_1(1 - D_2)(C_1I_2) + D_2(1 - D_1)(C_2I_1) + D_1D_2C_1C_2 \end{bmatrix} \tag{5}$$

In the above matrix, I have dropped the j subscript for clarity, and subscripts 1 and 2 refer to species 1 and 2. I_1 is the probability that species 1, when already present, allows species 2 to colonize. I_2 is the analogous probability for species 2. X_1 is the probability that species 1 displaces species 2 if both have successfully colonized. Competition is completely asymmetric so that species 2 does not displace 1. If displacement does not occur, competition does not affect fecundity.

For examples of the transition probabilities, the probability an empty patch remains in that state (first row, first column) is the probability that neither species colonize or $(1 - C_1)(1 - C_2)$. At the most complex extreme, the probability that a patch with both species stays in that state (fourth row, fourth column) is the sum of the probabilities that neither die nor displace the other, only species 1 dies but recolonizes, only species 2 dies but recolonizes, and both species die then recolonize.

For the multispecies interactive simulations, I present the results of a three-species model. Such a system is large enough to evaluate measures of diversity and to incorporate indirect effects among species, but not too large that determining the transition probabilities is unreasonable. The three species model is as follows:

$$\begin{bmatrix} P_e \\ P_1 \\ P_2 \\ P_3 \\ P_{12} \\ P_{13} \\ P_{23} \\ P_{123} \end{bmatrix}_{t+1} = \mathbf{B} \begin{bmatrix} P_e \\ P_1 \\ P_2 \\ P_3 \\ P_{12} \\ P_{13} \\ P_{23} \\ P_{123} \end{bmatrix}_t \tag{6}$$

where P_1 is the proportion of patches with species 1, P_{12} is the proportion of patches with species 1 and 2, and so on. \mathbf{B} is an eight-by-eight transition matrix with probabilities calculated as in \mathbf{A} (Eq. 4), except that in the three-species model, species 1 can displace species 2 and 3 (X_{12} and X_{13}), and species 2 can displace 3 (X_{23}). Also required is inhibition in patches occupied by pairs of species I_{12} , I_{13} , and I_{23} . For simplicity, I assume that the inhibition in patches with two species is the mean of that of the in-

dividual species [$I_{12} = (I_1 + I_2)/2$], and that $X_{12} = X_{13} = X_{23}$. From the state vector in Eq. 6, the mean patch species richness (α) in a neighborhood is

$$\alpha = P_1 + P_2 + P_3 + 2(P_{12} + P_{13} + P_{23}) + 3P_{123} \tag{7}$$

Effects of neighborhood scale inhibition and competition on spatial patterns

Increasing the amount of inhibition or competition reduced the steepness of the downstream gradients in population size and species diversity (Figs. 6 and 7). At the upstream end of the gradient, competition and inhibition were unimportant because only a small fraction of the patches could be occupied. Conversely, at the downstream end of the gradient, a much larger fraction of the patches were occupied and thus competition and inhibition restricted population size and diversity. Although the net effect of this is to reduce the steepness of the downstream gradients, even with $I = 0$ (perfect inhibition), or $X = 1$ (perfect competitive displacement), a strong gradient in species diversity remained.

Although downstream increases in diversity were robust to competition (Fig. 7A) and inhibition (Fig. 6), inferior competitors/inhibitors declined in the most downstream neighborhoods where competition or in-

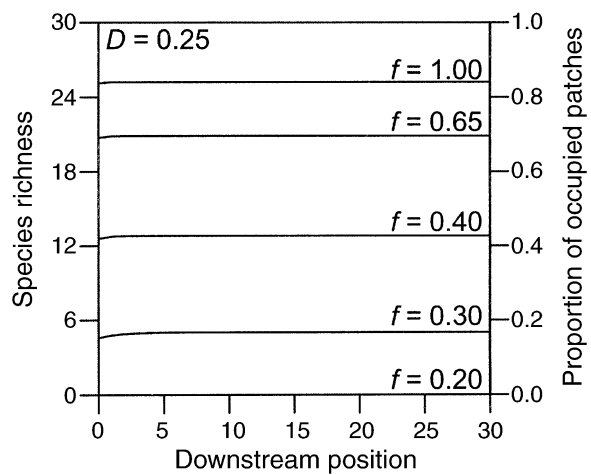


FIG. 5. Downstream gradients in species diversity and population size for a noninteractive community after 100 time steps with varying fecundity rates, a death rate of 0.25, and ineffective dispersal ($b_u = 5$, $b_d = 2.25$).

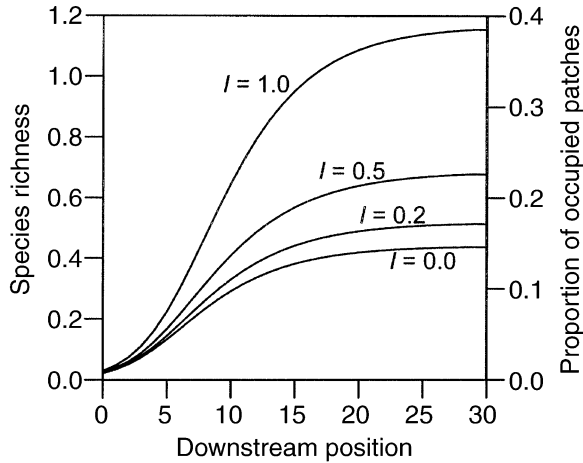


FIG. 6. The effects of varying inhibition, I , the probability that species can colonize an already-occupied patch. The three species model has been simulated for 100 time steps, no competitive displacement, $f = 0.38$, $D = 0.25$, $b_u = 2.5$, and $b_d = 0.5$.

hibition was most intense (Fig. 7C, D). To further evaluate depressed levels of the inferior competitor downstream, I ran a simplified version of the two species model (Eq. 4), modeled after Hastings (1980) and Tilman (1994), where the superior competitor is so effective at excluding or inhibiting the inferior that the two species never co-occur in a single patch. This was done by setting $I_1 = 0$, $I_2 = 1$, $X_1 = 1$ and setting to 0 the transition probabilities that the inferior competitor (species 2) can colonize or survive if the superior (species 1) colonizes.

I found that without any directionality to the dispersal ($b_u = b_d = 0.80$, Fig. 1A), the inferior competitor, if identical to the superior in dispersal, fecundity, and mortality rates, was invariably driven to extinction (Fig. 8A). However, if dispersal was equally effective, but occurred in a prevailing downstream direction ($b_u = 2.5$, $b_d = 0.5$), the species could coexist, even if identical in all noncompetitive traits (Fig. 8B). More specifically, the inferior competitor obtained a small refuge from competition at the upstream end of the gradient. Here, the effects of competition were minimal

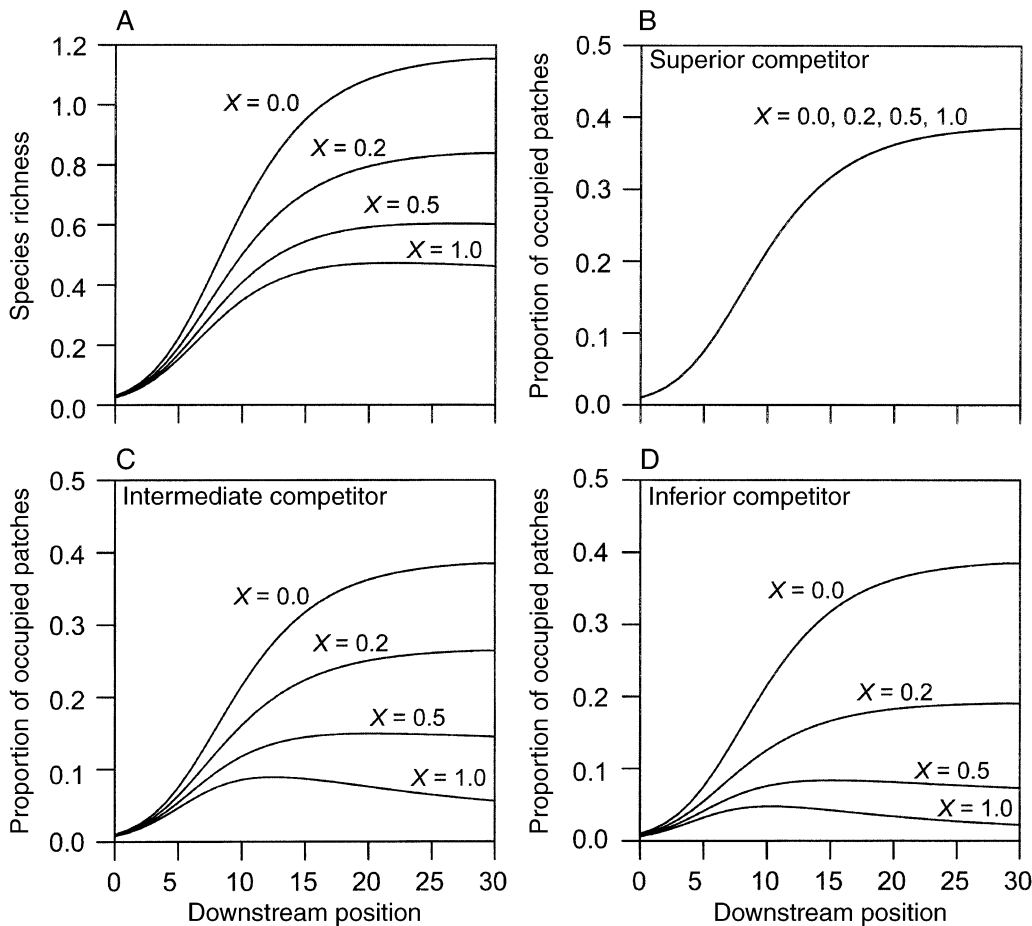


FIG. 7. The effects of varying competition, X (probability that one species displaces another) on (A) diversity, and the abundance of a (B) superior, (C) intermediate, and (D) inferior competitor in a three-species system. There is no inhibition in the simulations. The model has been simulated for 100 time steps, $f = 0.38$, $D = 0.25$, $b_u = 2.5$, and $b_d = 0.5$.

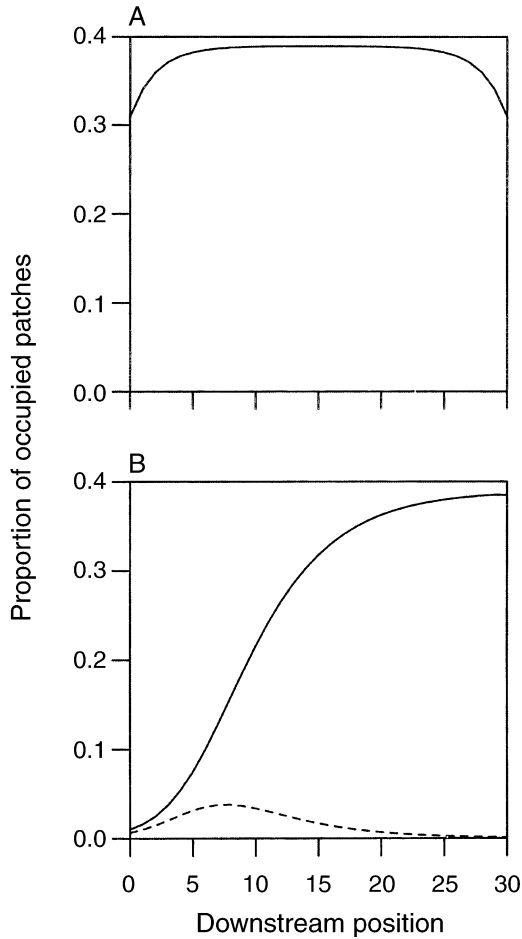


FIG. 8. Competition between two species in a system (A) without directional dispersal ($b_u = 0.80$, $b_d = 0.80$) and (B) with directional dispersal ($b_u = 2.5$, $b_d = 0.5$). The model has been simulated for 100 time steps, $f = 0.38$, and $D = 0.25$. The solid line indicates the abundance of the superior competitor, and the dashed line the inferior competitor.

because the better competitor could only occupy a small fraction of the available patches. At the downstream end of the gradient, the superior competitor obtained its maximum abundance, which like the situation in Fig. 8A, lead to the near elimination of the inferior competitor.

MODELS WITH DISTURBANCE

Periodic disturbances may be key to dispersal driven patterns because they create conditions of dispersal limitation. In order to examine how larger scale extinctions and disturbance influence the importance of directional dispersal, I simulated the model following a system-wide event. Modeled after a flood, the disturbance caused neighborhoods to suffer extinctions in unison, leaving only small source populations randomly scattered through the system. This changes the initial conditions in the model from a case where all species are in all neighborhoods, to one where each neighbor-

hood had some small probability (0.05) of containing a given species.

Disturbances that leave behind randomly scattered source populations relaxed the otherwise strict dispersal and growth rate conditions that emerged in Figs. 3 and 5 for a downstream gradient in species diversity (Fig. 9). Although in the long term, these simulations converged to the type of gradients seen in Figs. 3 and 5, at times prior to equilibrium, strong downstream gradients in diversity emerged even with fast growing and/or poorly dispersing populations (Fig. 9A, B). This is because the further downstream the neighborhood, the more likely it is to contain an upstream source of any given species. This gives downstream neighborhoods a head start in their postdisturbance recovery. This head start is driven by the relative abilities to disperse in the upstream and downstream directions, and not the overall effectiveness of dispersal. The downstream gradients in Fig. 9 emerged most strongly after 25 and 40 years depending on the parameter combinations. Though after 100 years, these gradients are eliminated, if system-wide disturbances occur at the appropriate frequency, these qualitative patterns could persist.

DISCUSSION

There is intuitive appeal to the notion that in systems where dispersal occurs in a primary direction, say downstream, that downstream areas should exhibit larger populations and more diverse communities than those upstream. The overall conclusion from the model presented here is that patterns of population size and species diversity may track the direction of dispersal, but only under certain levels of fecundity, death, dispersal, competition, and disturbance. It is not directional dispersal alone that drives patterns of population size and diversity. Rather it is directional dispersal, operating in conjunction with low population growth, competitive interactions, and disturbance.

For example, only when the fecundity and death rates were such that the individual neighborhoods were dependent on external propagule supply did downstream increases in population size and diversity strongly emerge in the long term. Also required was dispersal so effective that it may be restricted to riparian (Waser et al. 1982) or bird-dispersed plants, and marine benthic organisms (Roughgarden et al. 1988). This does not invalidate model predictions for species that disperse more locally, because they may have the same shaped dispersal kernels (Fig. 1B), but over smaller distances. Thus the spatial scale over which model predictions are relevant depends on the scale of dispersal. In addition, incorporating more complex dispersal kernels with "fat tails" (Wolfenbarger 1946, Clark 1998, Nathan and Muller-Landau 2000) can increase the range of demographic parameters over which directional dispersal drives downstream patterns (J. M. Levine, unpublished data).

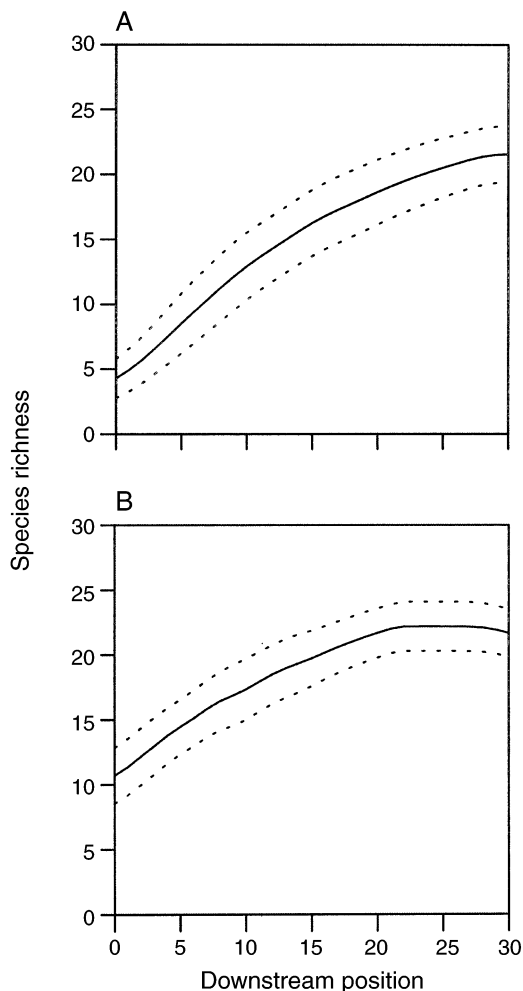


FIG. 9. Effects of a system-wide disturbance that leaves only randomly scattered small source populations on the downstream patterns of diversity in a 30-species noninteractive system. The solid and dashed lines show the mean \pm 1 SD of 100 simulations of the model (A) 20 and (B) 45 time steps after a system-wide disturbance where each neighborhood had a 0.05 probability of containing a source population for any given species. Dispersal and demographic parameters are such that (A) fecundity is too high for downstream increases in diversity to develop in the absence of disturbance ($f = 1.50$, $D = 0.25$, $b_u = 2.5$, $b_d = 0.5$), and (B) fecundity is too high and dispersal effectiveness too low for such patterns to develop in the absence of disturbance ($f = 1.50$, $D = 0.25$, $b_u = 5$, $b_d = 2.25$).

With appropriate demographic and dispersal parameters, neighborhood scale competition and inhibition reduced the steepness of, but never eliminated the downstream increases in species diversity (Figs. 6 and 7). At the same time, directional dispersal could strongly influence the outcome of competition. In our simulations, directional dispersal created severe recruitment limitation of the superior competitor in upstream neighborhoods, which resulted in coexistence in these regions. Yet in most patch models, the persistence of an inferior competitor requires that species to possess

a superior colonization ability (Hastings 1980, Tilman 1994, Levine and Rees 2002). Thus coexistence in directionally dispersing systems may be more complex than in systems where species disperse equally well in all directions.

Implications for the Eel River system

Results of a seed addition experiment in the plant community along the Eel River (Levine 2001) support the hypothesis that variation in seed supply is a major determinant of downstream increases in species diversity in the system. The model results presented here suggest two possible scenarios by which variation in seed supply contributes to downstream increases in diversity in the system. The system may be composed of a series of populations with highly effective long-distance dispersal, dependent on the external input of seeds for their persistence (Fig. 3). Alternatively, the system may be recovering from a large-scale disturbance, which left behind only scattered source populations (Fig. 9).

Empirical data from the field system better support the second hypothesis. Based on the dispersal of glitter seed mimics in the system, the plants do not disperse very effectively between patches (Levine 2001). In fact, dispersal is even less effective than is assumed in the Fig. 5 simulations, where downstream increases in diversity failed to develop regardless of species demographic rates. Other work in the habitat better supports the alternative hypothesis that the system shows downstream patterns because of past disturbance. The South Fork Eel River plant community is flooded annually, and though a typical winter of floods removes <0.5% of the tussocks and kills only a small fraction of the resident plants, the system was largely destroyed by the catastrophic 1955 and 1963 floods. Eye-witness accounts of the study stretch after these 100–1000-year-interval events indicate that the floods removed ~70–90% of the tussocks, likely leaving only small source populations of the various species. These past disturbances may be critical to current observations of a downstream increase in diversity in the Eel system.

Conclusions

Many ecological studies attempt to categorize systems as either propagule-limited or limited by safe sites, competitors, and other local processes (reviewed by Turnbull et al. 2000). In the current study, understanding the *degree* of propagule limitation was essential to understanding the importance of directional dispersal. I found that only the most propagule-limited systems, such as those dependent on external supply for persistence or those recovering from a system-wide disturbance, showed effects of directional dispersal on community patterns. This suggests that focusing less on whether or not a system is propagule limited, and more on the degree of limitation, may be fruitful in future empirical studies of propagule supply.

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